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A PROFESSOR'S STORY OF HYBRID CORN

by

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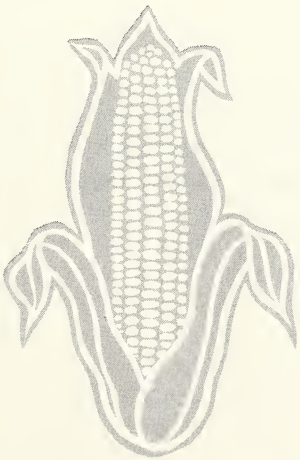

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PREFACE

As I approached the time of my retirement on June 30, 1952, several of my friends and associates suggested that I would now have time to write the history of hybrid corn. They said also that while the history as given by Crabb under the title, "The Hybrid-Corn Makers, Prophets of Plenty" was an interesting and worthwhile story, they thought it would be a valuable contribution if someone who had taken an active part in the basic research work of hybrid corn development would write a history that would emphasize the difficulties that faced early corn breeders, the many research problems that have been solved during the period of hybrid corn development which have played a large part in making hybrid corn a reality, and some of the possibilities of further improvement of hybrid corn.

My first two years after retirement from the University of Minnesota, starting in the fall of 1952, as a member of the Cornell team stationed at the College of Agriculture, University of the Philippines, were given over to the problems of aiding this college during its reconstruction period and more particularly of helping in the development of the Central Experiment Station of that college. While there had been an original appropriation in 1917 for the Experiment Station, no further direct appropriations for Experiment Station researches had been made. Many valuable agricultural researches have been carried out at the college but these have consisted largely of undergraduate thesis problems under staff members. In nearly all departments one or more of the staff have taken graduate training and in many instances in the United States.

The primary purpose of this reference to experiences in the Philippines is to make clear that, as a result of basic research in corn breeding, certain principles could be applied to the solution of the problem of producing adapted double-cross hybrids for the Philippines. Each of our Cornell group had a counterpart in his special research field. My Filipino co-worker, Dr. D. N. Umali, completed work for the Ph. D. at Cornell in 1946 with a major in Plant Breeding. On returning to Los

Banos, where the College of Agriculture of the University of the Philippines is located, to take charge of many phases of plant breeding researches, he started studies with the hope of developing hybrid corn for Philippine use. In the Philippines the field corn grown consists largely of Philippine tropical flint varieties of both yellow and white endosperm seed color. Waxy corn of similar type is grown extensively for eating, much as we use sweet corn.

Several undergraduate theses had been completed before my arrival, and two of these consisted of studies in inbred-variety crosses of general combining ability of approximately twenty selected inbreds. From these studies I helped Dr. Umali to select a few inbred lines of good general combining ability that appeared most satisfactory as inbreds and yielded well in inbred-variety crosses. One group of these came from College Yellow Flint, a Philippine variety that had a rather long history. Another group was from a variety called Cuban that had been introduced a few years earlier by Dr. Capinpin of the College. Both varieties had been grown and selected for several previous years and it was known that considerable hybrid vigor resulted from their F_1 cross.

Little attention had been paid to the seed characters of the inbreds. Therefore replicated trials of inbreds and of the possible F_1 crosses between them were studied as soon as seed for these purposes could be produced. To reduce the work so that it could be handled with the help available, it was decided, in conference with Dr. Umali, to use single crosses to predict the yield of double crosses primarily of the type (Cuban X Cuban) (College Yellow X College Yellow). There were many difficulties to be surmounted, such as isolated plots, seed drying and storage facilities, none of which were available when the Cornell - University of the Philippines contract was started in 1952 with funds made available by ICA.

It is of some interest that a wide collection of both inbred and varietal material was obtained from Mexico and Colombia through the help of the Rockefeller Foundation and especially through the kindness of Dr. Sterling Wortman, who at that time was in charge of their corn breeding program in Mexico. Breeding material from other sources of corn, especially from the United States with the help of Dr. M. T. Jenkins, was introduced. These are mentioned briefly to show that the breeding problems were considered from many different angles.

The F_1 crosses between inbreds of College Yellow and

Cuban were used as a basis of prediction of double-cross performance and for final trials of the double crosses. Certain of these tests gave results of great promise in comparison with open-pollinated seed from Cuban and College Yellow.

In addition to the breeding details it was necessary to make arrangements for wide testing throughout the Philippine Islands of these new double crosses. This led to a coordinated plan of breeding, testing, and the distribution of seed of improved varieties of hybrid corn and of rice by the College, and the Bureaus of Plant Industry and Agricultural Extension of the National Philippine Government.

Four double crosses have been selected and have been increased and introduced. They are being grown in a limited way, and so far there is every indication that they will serve to greatly increase production. As in the United States these new hybrids, of greater potential yielding value, have led to related studies which are also being developed on a cooperative basis. These include problems of seed processing, seed treatment, the development of seed drying and storage facilities, and other problems of crop production including the use of commercial fertilizers, crop rotation, cultivation methods, and weed control.

One of my pleasant memories and treasured experiences was a letter from Dean L. B. Uichanco under date of July 20, 1956. He wrote, "Doctor Umali may have written you that your leadership, enthusiasm and diligence in rice and corn breeding while here with us are now beginning to yield their first dividend, when at last we can start to make available to the farmers on a limited scale hybrid corn that works satisfactorily under Philippine conditions and which has outyielded the ordinary corn by 120 percent." It seems probable, with more complete and adequate tests, that the increase in yield may not be as great as this. It also seems probable that these first introduced hybrids will pave the way for the eventual wide use of hybrid corn in the Philippines which will have as great value as a source of increased and more efficient production as hybrid corn has had in the United States.

These results were obtained rather quickly in the Philippines by the direct application of corn breeding principles that resulted from the many basic breeding studies in our country. They furnished a part of the inspiration for the writer's story of the history of hybrid corn.

Many corn breeders and others interested in hybrid corn very kindly have made available certain information that has been requested. Others have stated their views in relation to future hybrid corn developments. In many cases it has been possible in the text to give credit to those who have made the information available. In respect to the present status of research and breeding studies the writer's viewpoint has been modified by discussion with others. There has been no attempt to make a complete review of literature by citing all published papers although as far as possible all important contributions have been read. Those reviewed in the history as presented have appeared to the writer to be of value in basic or applied research that has been of fundamental importance in the development of hybrid corn. Administrative leaders of the Institute of Agriculture on the St. Paul Campus of the University of Minnesota, including Drs. H. Macy and T. H. Fenske, have read the manuscript. Several valuable suggestions have been utilized. However, the writer alone is responsible for the presentation of this history in its present form.

Special acknowledgment is made to Dr. Will M. Myers, Head of the Department of Agronomy and Plant Genetics, University of Minnesota, who has critically read the text, has made very valuable suggestions relating to plant breeding interpretations, and in relation to the manner of presentation. Dr. E. H. Rinke, of the same Department, also was very helpful. Dr. Emmett Pinnell, Head of the Department of Field Crops, College of Agriculture, University of Missouri, read the completed text and made several valuable suggestions. To my wife, Rachel Rude Hayes, I am very grateful for continued aid during the preparation and completion of the Hybrid Corn Story.

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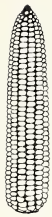
Chapter 1  THE ORIGIN OF CORN AND OF CORN HYBRIDS

Introduction

The writer has observed almost the entire history of hybrid corn and has taken part in its development. His own work in this field has covered a period of about forty-seven years. Today hybrid corn is grown commercially for the greater part of the acreage in the United States and is being developed for use in other countries, including Mexico, Canada, and corn-growing areas of South America, Europe, Asia, and Africa.

Origin of Corn

Many students of the origin of crop plants have accepted the hypothesis of the Russian scientist, Vavilov, that the region of greatest diversity of types is usually the region of origin.

Mangelsdorf and Reeves (1939, 1959), Mangelsdorf (1947), and Mangelsdorf and Smith (1949), have made extensive studies of the origin of corn, and their conclusions have been rather generally accepted, although others have different viewpoints regarding certain phases. The views of Mangelsdorf and co-workers have been followed in this summary.

It has been concluded that cultivated varieties of corn have arisen from a wild pod corn that itself had a remote grass-like ancestor which gave rise on the South American continent in the lowlands of Paraguay, Northeastern Bolivia or Southwestern Brazil, to a single species, *Zea mays*, Indian corn, and on the North American continent, in Central and North America, to *Tripsacum*. This latter genus has a tendency to polyploidy and

to a perennial habit of growth. Mangelsdorf and Reeves, using a special technique, found it possible to hybridize *Tripsacum* and *Zea*. They have concluded that *Euchlaena*, teosinte, the third American genus of the tribe *Tripsaceae*, was produced by hybridization from crosses between *Tripsacum* and *Zea*.

Farquharson (1957) writes, "It has been shown that the cross between tripsacum and corn is not difficult to make, and requires no special technic. In fact it seems highly probable that this cross has occurred occasionally in nature. The hybrid plants go long unnoticed because of the close resemblance to tripsacum." He shows pictures of a cross of tripsacum, *T. dachyloides*, and Puno, a primitive Indian variety from Peru. This and similar crosses are evidence for his belief that such crosses may occur in nature.

The annual form of *Euchlaena*, like *Zea*, has ten pairs of chromosomes, although there is a perennial form with twenty pairs, while *Tripsacum* has eighteen pairs of chromosomes. *Zea* and *Euchlaena* cross readily and are very similar in chromosome structure.

Thus maize varieties of North America are supposed to comprise two main groups, (1) pure maize, which descended from wild pod corn, and (2) *Tripsacum* contaminated maize.

The oldest available fossil ear of corn was found in New Mexico's Bat Cave, dating from about 2000 B. C. This ear was very small, not much over an inch in length. Wallace and Brown (1956) describe studies of succession and distribution of fossil pollen taken from drill cores from old lake beds. These were reported in Botanical Leaflets of Harvard University in 1954. Corn pollen that was obtained from an old lake bed underneath Mexico City from a depth of sixty-nine meters has been estimated to be sixty thousand years old. It was said to be almost identical with the pollen of modern corn.

Wellhausen and others (1951) observed over 2000 introductions and discussed the origin of twenty-five races of maize in Mexico. They concluded that the most ancient corn of Mexico was both a pod and a pop corn. Extensive crosses with exotic corn from the South, and with *Euchlaena*, and the conditions in Mexico of geographic isolation, have led to a wide range of types. These various factors have made Mexico a secondary region of origin of corn.

There are seven major groups of corn; pod, pop, flint, dent, flour, sweet, and waxy.

Each kernel of Pod corn is enclosed in a husk and the ear

also is enclosed in a husk as with other groups. The kernels may resemble those of any of the other groups.

Pop corn contains only a small amount of soft starch, which in many cases is generally around the germ, the major part of the starch cells being of corneous type.

Flint corn comprises varieties with starchy endosperm in which the soft starch is surrounded by corneous starch. There are both temperate and tropical forms of flint corn. Most of the temperate region varieties, such as New England flints, stool very strongly, while tropical flints often have few or no basal suckers.

The Dent corns are characterized by having the corneous starch at the sides of the kernel while the soft starch extends to the summit. The soft starch dries more rapidly than the corneous, causing the characteristic indentation of the kernel.

The Sweet corns are characterized by a translucent, horny appearance of the kernel and a wrinkled condition when dry. East (1909a) concluded sweet corn varieties were of dent, flint, or of pop origin that had lost their ability to produce starch. The few starch grains produced are small and angular. Sweet corn varieties selected and bred in recent years, including many of the hybrids available, excel in having a very tender pericarp.

The Flour corns are characterized by an almost complete lack of corneous starch, although many and perhaps most flour corns produce a small amount of corneous starch. They seem to the writer to be as closely related to flint, dent, or pop corn as are sweet corns. Some varieties of flour corn carry a small amount of corneous starch on the cap of the kernel, and resemble flint or pop corns in this respect, while others carry this corneous starch on the sides of the kernel like dent corns. Flour corns of dent type have a slight indentation of their kernels.

The Waxy corns are characterized by an endosperm of waxy nature resulting from a carbohydrate of a different form from that in starchy varieties. The original source is China, but waxy seeds, like sweet or other recessive types, have occurred by mutation in experimental cultures.

In the Philippines, waxy types of corn are grown extensively and cooked in the husks much like we use sweet corn. As waxy corn is grown so widely for this purpose, a large part of the native Philippine tropical flint varieties are contaminated with kernels of waxy endosperm.

The Origin of Corn Belt Varieties

The origin of American corn varieties is of considerable interest to the corn breeder. The book entitled, "Corn and Its Early Fathers," by Wallace and Brown is a fascinating story of the early history of corn in the United States. It presents the biology of the corn plant in non-technical language. It also outlines the early studies of corn, with descriptions of the persons who led in these fields. It seems very clear that corn varieties in the Corn Belt originated by selection from crosses of a New England 8-rowed flint with a late, many-rowed gourd-type dent. Such a broad basis of parentage furnishes a logical reason for the wide diversity among varieties. It seems of special interest to the writer that Edgar Anderson, well-known botanist of the Missouri Botanical Gardens at St. Louis, who completed his graduate training under Dr. East's direction, collaborated with William E. Brown (1952) in the history of the origin of varieties in the Corn Belt.

The Value of Hybrid Corn

Various comparisons have been made to show the value of hybrid corn. During world war II increased production played an important part in winning the war. In more recent years there has been an over-production of many agricultural crops which has led to a curtailment of acreage, the establishment of government control and the reduction of acreage. In spite of these controls the total production of corn has increased and the storage of grain by the government has constantly increased. Total acreage of corn, production in bushels, and yields per acre are summarized in Table 1 from Agricultural Statistics as presented by the U. S. Department of Agriculture (See Table 1).

The acreages grown were over 100 million in the first two periods 1920-24 and 1930-34. In 1940-44 only about 90 million acres of corn were grown, and in 1950-54 and 1955-59 the acreage dropped to 82+ million and 78+ million, respectively.

Total yields, however, have tended to increase. The average production in various periods is of interest. Thus, in 1920-24, 2.7+ billion bushels were produced. In 1930-34 total production dropped to about 2.3 billion bushels. Only a very

small acreage of hybrid corn was grown and there was a period of severe drought. In 1940-44 total production was about the same as in 1920-24 with an average during 1940-44 of 2.8+ billion bushels. In 1950-54 and 1955-59 when acreages dropped from over 100 million in the early period of 1920-24 to 82+ million and 78+ million, respectively, total production increased and the average production in bushels was 3.1+ billion and 3.6+ billion bushels.

Yields in bushels per acre for the five periods were 27.2, 21.9, 31.9, 38.5, and 47.3, respectively, and in 1960 and 1961, which were very favorable years for corn, the acre yields were 60 or more bushels, on the average. These yields as given reflect the overall value of hybrid corn. As has been stated, in connection with other presentations given later, all of this phenomenal increase is not due to heredity. With the advent of hybrid corn there also have been improvements in agronomic technics leading to better stands due to high grade seed, better planting methods, control of weeds, improved fertilization practices, disease and insect control, and adequate machine methods that have played a part in all phases of growing and handling of the crop.

It seems probable to the writer that the value of hybrid corn can be better appreciated by comparing the yields of oats and corn in the United States and the summary of the extent to which hybrid corn has been grown during comparable years. For this purpose the yields per acre of oats and corn are summarized for four different years, 1929, 1939, 1949, and 1959, respectively. The per cent of acreage planted to hybrid corn is given also for each of the four years. (See Table 2).

Table 1 Acreage, Production in Bushels, and Yields in Bu. per Acre of Corn (United States)

Years Av.	Acreage: 1000	Production Bushels in 1000 Terms	Yield Bu.
1920-24	101,280	2,761,753	27.2
1930-34	103,944	2,289,614	21.9
1940-44	90,833	2,846,312	31.9
1950-54	82,425	3,112,103	38.5
1955-59	78,661	3,657,879	47.3

Table 2 Acre Yields of Corn in the United States

Year	Oats		Corn		Per cent Hybrid Corn
	Bu. per Acre	In % of 1929	Bu. per Acre	In % of 1929	
1929	29.2	100	25.7	100	0
1939	28.6	98	29.7	116	22.9
1949	32.3	107	37.8	147	78.3
1959	37.7	129	51.5	200	94.8

Although the acre yields of oats improved during the periods indicated and in 1959 was 29 per cent greater than in 1929, the increased yield is small in comparison with corn. It is recognized that corn usually occupies the more desirable acreage and that oats are often planted on less desirable land; however, there has been a significant increase in the yield of oats. This also is partly a result of better breeding, although oats being a self-pollinated plant, it so far has been impossible to utilize hybrid vigor.

With corn, however, there is a direct comparison of yields in these four years in relation to the per cent of the crop planted to hybrid seed. Thus, in 1929, practically none of the acreage was hybrid. In 1939, 22.9% of the total acreage in the United States was planted to hybrid seed, and in 1949 and 1959, respectively, the hybrid seed acreage in the United States rose to 78.3% and 94.8%. At the present time all of the field corn acreage in Iowa and Illinois is planted to hybrid seed and several states, including Minnesota, have percentages of 99 or over.

If one takes the bushel yield of corn per acre in 1929 as 100, the yield percentages in 1939, 1949, and 1959 become 116, 147, and 200 respectively. A large part of these increases result from the utilization of hybrid vigor.

How Hybrid Seed Corn is Produced

Although Shull, as will be presented later, outlined the value of selected single crosses between inbred lines as a means of producing high yields of corn in comparison with commercial varieties, seed production for the commercial crop from single crosses of inbred lines did not appear to be a satisfactory means

for practical use, as the inbred parents were low in productivity. Later Jones proposed the double-cross plan which is now used extensively by the seed producer.

The method for each double-cross hybrid consists of developing four inbred lines that yield well in all six possible single crosses, especially in the four singles not used as parents in the double cross. These inbreds are selected also for ability to withstand lodging, for other desirable characters including insect and disease resistances and for adaptation to the environmental conditions where the particular hybrids will be grown. The female single-cross parent is selected also on the basis of ability to produce seed of satisfactory quality and plantability. With the advent of mechanical methods of handling the crop, attention has been given also to producing a hybrid that is adapted to mechanical harvesting without loss of ears. For commercial seed production of double crosses, two single crosses are used as parents and these are crossed to produce double-cross seed that is sold to the corn grower.

As will be emphasized later in presenting the effects of self-fertilization, all inbred lines are greatly reduced in vigor in comparison with normal corn. First generation crosses between inbreds that differ in genetic factors for growth characters have restored vigor in most F_1 crosses, and certain crosses of selected inbreds often yield much more than normal open-pollinated corn.

It is not generally appreciated that many single crosses do not yield more than normal corn. Thus, if one has a random selection of inbred lines from a corn variety and makes crosses at random between these inbreds, approximately half of the single-cross combinations will yield less than the normal variety.

Single crosses are produced by alternate planting of two inbred lines in an isolated plot and detasseling plants of the inbred to be used as the female. A common rate of planting is two rows of the female to a single row of the male. The double-cross seed is produced by planting the single-cross parents in an isolated plot, and here the ratio of female to male rows is usually 3:1 or 4:1, although a common practice is to alternate six rows of the female with two of the male. The double cross has the advantage over the single cross in that the yield of seed in the crossing plot is much greater than from the inbred parents. The somewhat greater variability of the double cross than the single cross causes it to have a wider region of adaptation.

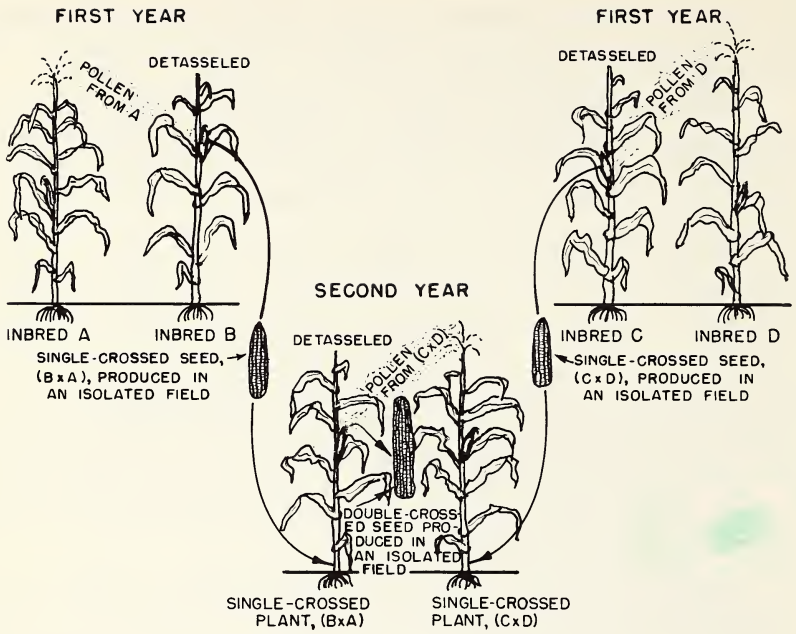
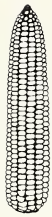


Figure **1**

A diagrammatic illustration of the double-cross plan of seed production, after four inbreds, A, B, C, and D have proven by previous trial to produce a desirable double cross of the nature (A x B) (C x D). The inbred lines must be maintained by controlled pollination. Three different crosses are made to produce double-cross seed to be used by the commercial grower. There are two single crosses, (A x B) and (C x D). These each are made by growing the two inbreds for each single cross to be made in alternate rows, and detasseling the inbred to be used as a female before silks appear on that inbred. Double-cross seed is produced by planting the two single crosses to be used as parents in alternate rows and detasseling one of the single crosses as illustrated for (B x A) in the diagram. (Courtesy of H. H. Hughes and I. J. Johnson, Iowa State College.)

To gain the greatest benefit from hybrid corn the commercial grower each crop season uses hybrid seed that has been produced in a crossing plot from a cross of known performance. Much of the benefit of hybrid corn is due to the fact that all plants of the hybrid have similar capabilities for excellent performance.

With sweet corn, for canning and freezing, a single cross between two inbred lines often is used, since uniformity and quality are so important with this type of corn. Such single crosses are used extensively also for home gardens, although uniformity of maturity is of doubtful value in this case.

Chapter 2  EARLY STUDIES OF SHULL, EAST AND HAYES

Early Studies of Shull and East

Dr. E. M. East, at the Connecticut Agricultural Experiment Station, and Dr. G. H. Shull, at Cold Spring Harbor, started studies of inbreeding and cross-breeding in corn, and in 1906 they grew lines from seed that was produced by one previous season of self-pollination. Even after reading Crabb's[1] (1947) description of seed sent by Love to East at Connecticut from the self-pollinations at Illinois, it seems to the writer that Dr. East's records of the extent of self-pollination of his Leaming inbreds should be accepted. I have concluded, therefore, that East preferred at Connecticut to start with inbred material of the Leaming lines that had been selfed only once.

East and Shull both independently concluded that the use of hybrid vigor for the commercial crop eventually would be developed. The early history of hybrid corn is based to a large extent upon the studies of these two research leaders.

While the research studies of Shull and East were conducted independently, they were familiar with each other's work. My first meeting with Dr. Shull was in the summer of 1909. Tschermak, one of the rediscoverers of Mendel's Laws, and von Rumker, a well-known German plant breeder, visited Dr. East at Griffin, Connecticut where our corn experiments were carried on. Dr. Shull was also a visitor on that day. It was a thrill for me to be present and listen to their disucssions in the corn field and also in our offices.

[1]Crabb stated that the inbreds received by East from Illinois had been selfed for more than a single season.

The chapter entitled, Modern Science Comes to Corn, in "Corn and Its Early Fathers," by Wallace and Brown emphasizes the importance of the rediscovery of Mendel's work and methods, the early studies of Beal and others, and discusses in somewhat greater detail the contributions of Shull and East. It seems desirable here to outline briefly some of their conclusions relating to the work of these two men. Both Shull and East found that inbreeding produced uniform lines that were greatly reduced in vigor. The writers concluded that East had more desirable inbreds than Shull. The latter, however, was impressed with the value of single crosses between inbreds, while East thought that varietal crosses would have greater practical value. Wallace and Brown state, "Both men were doing essentially the same thing, for the same reasons and at the same time, East being more influenced by Darwin, and Shull by Mendel." The latter part of this conclusion seems wrong to the writer, and this was one reason for the brief review later of the bulletin by East in 1907. While East appreciated the importance of the biological studies of many early students and was greatly impressed with the studies of Darwin on cross- and self-fertilization, he, as well as Shull, appreciated that Mendel's Laws and methods of study furnished the basis for plant breeding applications. Shull, like East, was well grounded in biology and a great admirer of Darwin.

A biographical memoir of Edward Murray East was published by Jones (1945b). This seems to the writer to be an excellent summary of the life and accomplishments of this early leader in genetics and plant breeding. Jones presents in considerable detail correspondence between Shull and East. Although East's (1908) first paper on "Inbreeding in Corn" was published prior to Shull's (1908) first paper, "The composition of a field of maize," it seems evident that East attended a meeting of the American Breeders Association held in Washington, D. C. on January 28-30 in 1908 when Shull presented the paper and that Shull lent the manuscript to East. In a letter written by East to Shull it was stated that East agreed with Shull's conclusions that inbreeding brought out homozygous characters. In later correspondence East wrote, "I freely admit that your paper of 1908 gave me the first idea of inbreeding separating the biotypes and that on this hinges the whole matter."

The following year East (1909b) submitted his next basic corn research paper to the American Naturalist entitled, "The distinction between development and heredity in inbreeding."

Figure 2

From left to right, Dr. D. F. Jones and former Vice-President H. A. Wallace. At the Donald Jones Field Day in 1950 Henry Wallace emphasized the leadership of former Director E. H. Jenkins at the Connecticut Agricultural Experiment Station, which was considered of primary importance in relation to numerous basic researches. He also emphasized researches that led to hybrid corn, and summarized major contributions of Jones. (Courtesy of D. F. Jones.)

Shull's (1909) second paper entitled, "A pure line method of corn breeding," was published in the American Breeders Report. In discussing these two papers East in a letter to Shull wrote, "I thought my idea of distinction between deterioration due to recombination of hereditary characters and that due to the depriving of the homozygote of the stimulus due to a cross was a new idea." He also wrote after reading Shull's second paper that he believed Shull had a similar idea, "but you did not express it in your first paper and do not make it clear in the second paper." East pointed out that this surprised him as he thought it the most important part of the whole matter. Although Shull made the statement in a letter to East that he cared little for priority the writer's contact through the years leads him to believe that both East and Shull were rather desirous of receiving credit for research accomplishments. In this respect they had I believe much the same viewpoint as other research workers. Both men belived their primary interest was in basic research, both were anxious that such research would lead to practical applications.

It is perhaps of doubtful value to attempt to decide whether East or Shull contributed more to corn breeding. As many writers have given greater credit to Shull who suggested the use of F_1 crosses between inbreds, it seems of interest to quote the viewpoints of Wallace and Brown. They speak of Shull as one of the earliest followers of Mendel. There were other leaders[2] in the new Mendelian methods, such as East, both in this country and in Europe, as, of course, Wallace and Brown well know.

It seems probable that Shull, as was stated by Wallace and Brown, "was perhaps the first to arrive at a clear concept of hybrid vigor." However, these writers conclude, "We believe that priority in pointing out the importance of inbreeding as a technique in corn-improvement belongs to Shull, but we feel corn breeders have been influenced more extensively by Edward Murray East."

[2]Bateson, in England, and co-workers worked with various organisms. Bateson's "Mendel's Principles of Heredity," published in 1909, was one of the earliest books known to the writer that summarized many of the cases of both simple and more complex forms of Mendelian inheritance known at that time. Bateson was responsible for much of the early Mendelian terminology. Spillman at Washington State about 1902 is considered by many to have independently rediscovered Mendel's Laws. He studied fourteen different wheat crosses. Reciprocal crosses were alike in F_1. Usually F_1 crosses were uniform and segregation occurred in F_2. He wrote, "In every case but one, which is noted later, the forms in each plot were simply combinations of the characters of the parental forms." He also wrote, "The types that tend to occur in the second generation, include all possible combinations of the characters of the two parents."

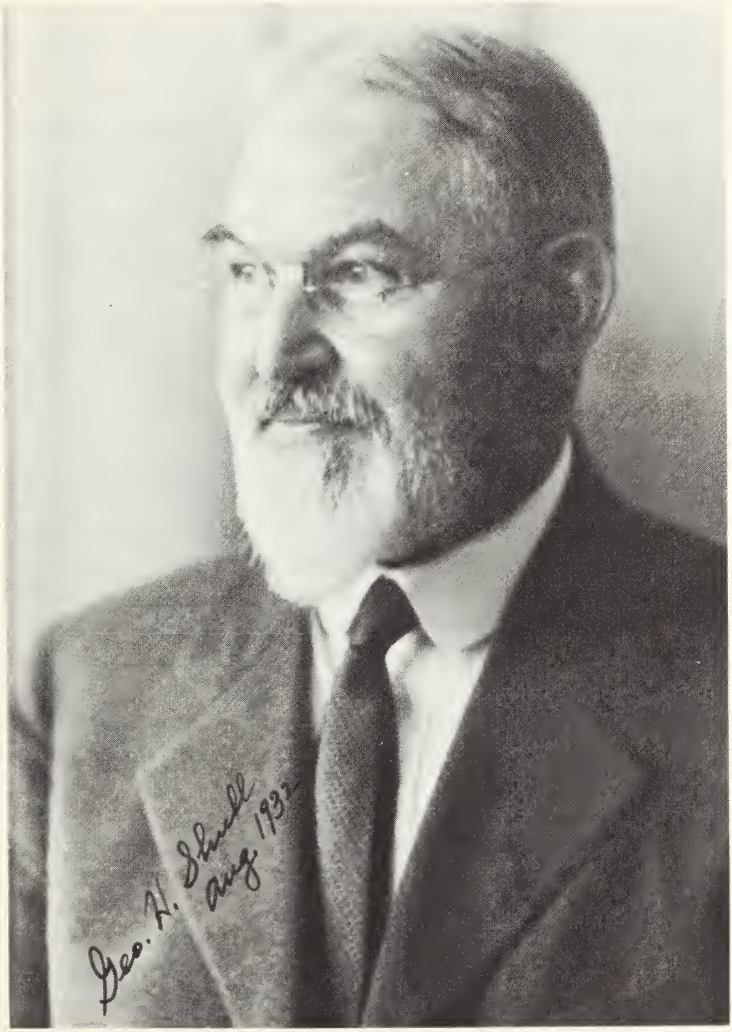


Figure 3 The late Dr. G. H. Shull who carried out important basic studies in relation to corn breeding at Cold Spring Harbor from 1904 through 1912. Dr. Shull for many years was a Professor at Princeton. Photograph taken by the late Dr. F. R. Immer in 1932 at the Genetics Congress at Cornell University.

Wallace was the chief speaker at the Donald Jones recognition day at the Connecticut Agricultural Experiment Station Day in 1950. His address entitled, "Double Cross Hybrid Corn. A Story of Small Plots and Big Men," (Wallace 1956) describes early researches in Connecticut. In discussing a visit with Dr. East at the Bussey Institution in 1925, he writes, "As I sat around and talked with East in the evenings, I found him cynical, irascible, prejudiced, warm hearted, stimulating and utterly charming." I might add that he was greatly interested in following the activities of his students. Several years after I left Connecticut he wrote me briefly that Sturtevant, a leading drosophila geneticist, told him that he thought my work in plant breeding was outstanding. I cite this to show that East kept rather close contact with former students and did not fail to pass on a complimentary statement when there was an opportunity.

An Early Paper by East

An early publication of East (1907) is of sufficient interest to deserve special comment, not only in relation to hybrid corn, but of even greater interest to the early development of plant breeding in the present century. This Connecticut Experiment Station bulletin was entitled, "The Relation of Certain Biological Principles to Plant Breeding." It is an admirable discussion of the biological principles of Lamarck, Darwin, Weismann, De Vries, Johannsen, Mendel and their contemporaries in relation to plant improvement. It relates biological principles to the studies of Vilmorin and others with sugar beets, to the selection studies of Le Couteur and Shireff in the latter part of the nineteenth century with small grains that emphasized the value of individual plant selection, to the work of Hopkins and associates on selection for chemical characters of corn for protein and oil content, to the extensive studies at Svalof by Nilsson and his coworkers and to other early studies at American Experiment Stations, especially at Cornell and Minnesota. These studies emphasize the Vilmorin Isolation Principle that the only way to determine the breeding value of a plant is to grow and examine its progeny. The value of hybridization was discussed also and special attention was given to early studies of Kölreuter, Knight, and Darwin. The Knight-Darwin law was quoted, "Nature abhors perpetual self-fertilization." Many workers at this time appreciated the new principles as presented by Mendel. A section of

the bulletin outlines East's views of the value of these laws as a basis for breeding improved varieties of crop plants.

Summary of Dr. Shull's Studies

A detailed history was given in 1952 under the title, "Beginnings of the Heterosis Concept," in Chapter 2 of the book entitled, "Heterosis."

This 1952 summary by Shull of his corn researches from 1904 through 1912 presents a complete picture of his studies with corn and deserves special comment. In the fall of 1904 Shull classified 524 ears of dent corn for row number, in 10 to 24 ear-row classes. In 1905 seed from ears from each row-class was planted in progeny rows. Selection for the original row number of each row-number class was continued by selfing within the line. Within each line also controlled cross-pollination was practiced. Photographs are presented showing representative ears in the fifth generation of selfing and of crosses within each line. He shows also from more than 50 plant progenies the best 11 ears of the highest yielding selfed line, from crossing within a line, and from the highest yielding F_1 cross between two selfed lines.

The early publications of Shull (1908, 1909, 1910, and 1911) were concise summaries of his studies. Major conclusions were that a variety of corn was composed of biotypes that should be studied in hybrid combination as presented in the 1908 paper. Methods of continuing to produce pure-line inbreds and for the production of single-cross seed were presented in 1909. Shull appreciated the economic difficulties of producing single cross seed and emphasized the importance of study by Agricultural Experiment Station workers of the practical value of such hybrids. The 1910 paper gave a short, concise summary in twelve statements of the effects of self- and cross-fertilization comparing inbreds with the F_1 and F_2 generations. In 1911 Shull discussed genotypes of maize and referred to Bruce (1910) who explained hybrid vigor on the assumption that this was due to favorable dominant elements. At this time neither East nor Shull accepted a Mendelian explanation of hybrid vigor. Both related heterosis to the heterozygous condition due to a physiological stimulus from hybridity.

A summary of the conclusions of Shull on the effects of self- and cross-fertilization as observed from his intensive

studies gives a rather clear picture of his results. The following is quoted from Dr. Shull's paper in 1910.

1. The progeny of every self-fertilized corn plant is of inferior size, vigor, and productiveness, as compared with the progeny of a normally cross-bred plant derived from the same source. This is true when the chosen parent is above the average conditions as well as when below it.

2. The decrease in size and vigor which accompanies self-fertilization is greatest in the first generation, and becomes less and less in each succeeding generation until a condition is reached in which there is (presumably) no more loss of vigor.

3. Self-fertilized families from a common origin differ from one another in definite hereditary morphological characters.

4. Regression of fluctuating characters has been observed to take place away from the common mean or average of the several families instead of toward it.

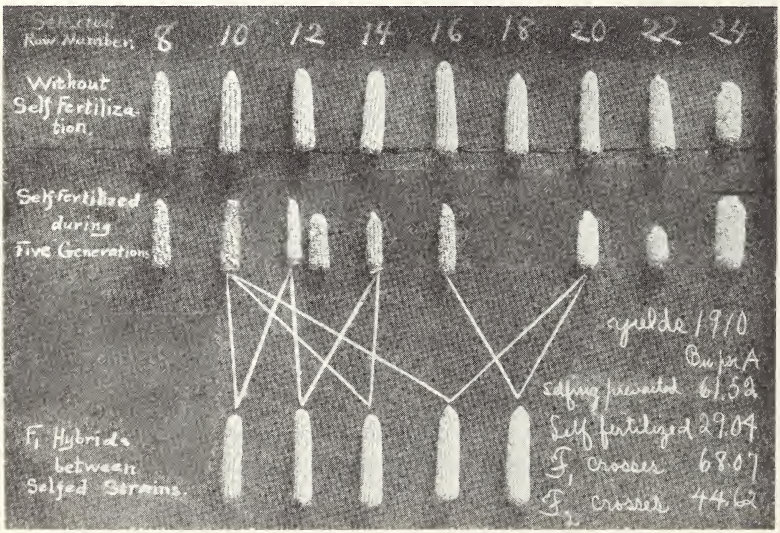

Row Numbers 8 10 12 14 16 18 20 22 24
Without Self Fertilization
Self fertilized during Five Generations
F1 Hybrids between Selfed Strains.
selfing reduced 61.52
Self fertilized 29.09
F1 crosses 68.07
F1 crosses 44.62

Figure 4 An exhibit in the Plant Breeding Department at Cornell University as set up in 1910. The upper row were original ears of 8 to 24 rows each of an open-pollinated dent corn variety. The middle rows are ears of inbreds selfed for five generations, and the lower rows are ears of five F_1 crosses. (From "Heterosis", Dr. Shull's paper, 1952)

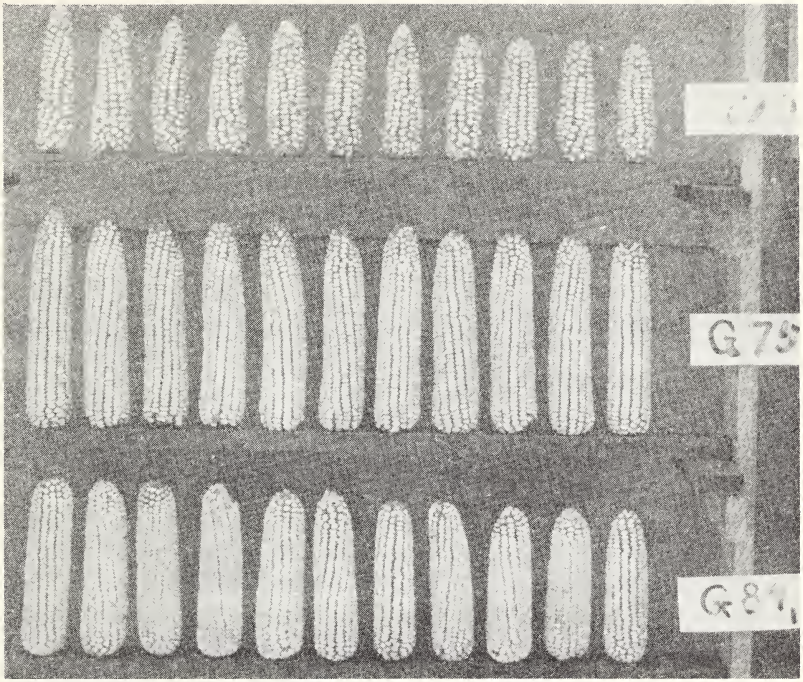


Figure 5 The upper row represents the 11 best ears of the best inbred from a progeny of 50 plants. The central row, the 11 best ears of the best F_1 hybrid, and the lower row, the 11 best ears of the original strain, or ear, that has been cross-bred by sib pollination during five generations. In each of the two latter cases 50 plant progenies were grown. (From "Heterosis," Dr. Shull's paper, 1952)

5. A cross between sibs within a self-fertilized family shows little or no improvement over self-fertilization in the same family.

6. A cross between plants belonging to two self-fertilized families results in a progeny of as great vigor, size, and productiveness as are possessed by families which had never been self-fertilized.

7. The reciprocal crosses between two distinct self-fertilized families are equal, and possess the characters of the original corn with which the experiments were started.

8. The F_1 from a combination of plants belonging to certain self-fertilized families produces a yield superior to that of the original cross-bred stock.

9. The yield and the quality of the crop produced are

functions of the particular combination of self-fertilized parental types, and these qualities remain the same whenever the cross is repeated.

10. The F_1 hybrids are no more variable than the pure strains which enter into them.

11. The F_2 shows much greater variation than the F_1.

12. The yield per acre of the F_2 is less than that of the F_1.

In 1914 Shull discussed inheritance of capsule form in *Bursa bursa pastoris*. Segregation ratios were given and explained on the basis of duplicate factors as had been done previously by Nilsson-Ehle (1909) for grain color in cereals and by East (1910) and East and Hayes (1911) for endosperm color in corn. This paper by Shull suggested the use of the term, "heterosis," for hybrid vigor and also suggested the desirability of such a term because hybrid vigor did not seem at that time to be explained satisfactorily on a Mendelian basis.

Organization of Work in Connecticut

The writer joined the staff of the Connecticut Station as an assistant of East on July 1, 1909. Dr. East already had accepted a position at the Bussey Institution of Harvard University but would continue at Connecticut until the fall of 1909. I would have the privilege in the winter of taking Connecticut work to the Bussey and enrolling as a graduate student. This plan was followed until the end of June in 1911, and during this time Dr. East continued to direct the corn and tobacco genetic experiments of the Connecticut Station. After that I was placed in charge, although Dr. East very kindly agreed to act as my adviser and continued in this capacity until I accepted a position at Minnesota on January 1, 1915. Several times each year during both the summer and winter Dr. East spent a few days in Connecticut so that he could observe and advise regarding the genetic and breeding experiments. Dr. D. F. Jones was my successor. I remained in Connecticut from September through December of 1914 to summarize previous work. Dr. Jones therefore had available material from the corn program at Connecticut which was started by Dr. East in 1905. Dr. Jones also took graduate work at Harvard under Dr. East's direction and for several years Dr. East advised regarding the continuation of Jones' studies. A major part of Dr. East's studies with corn were carried out at the Connecticut Station, although several phases were completed while

he was at the Bussey.

An interesting phase of the paper by Wallace (1956) was his explanation of the early successful studies at the Connecticut Station. He credits Director E. H. Jenkins with unusual capacities of administrative leadership. His ability to select outstanding men, and even with limited facilities, to instill enthusiasm in his staff and furnish a favorable environment for basic studies in plant breeding and other fields, was emphasized. The writer joins in paying tribute to Director Jenkins. Administrative leaders, like Dr. Jenkins, were not often available in these early days. I learned from Drs. Jenkins and East the importance of selecting research workers with good training and enthusiasm for their work, and the necessity of providing them with full opportunity to carry out their researches in the manner which seemed to them most desirable.

During the summer of 1909 the writer lived with East at a tobacco plantation at Griffin, Connecticut, where East's corn and tobacco experiments of the Connecticut Agricultural Experiment Station were being conducted during the crop season. The writer will always remember that summer. East was threatened with a nervous breakdown. Our days consisted of work in the fields for a few hours followed by periods of rest many of which were used by East to explain laws of heredity to his new assistant. The writer's interest in plant breeding is dependent largely on the capabilities of East as a teacher and research worker. In talks with him the field of plant breeding seemed an interesting and worthwhile occupation, although East was interested primarily in research on genetic principles.

Investigations of East and Hayes

East's early studies on corn breeding were published in reports of the Connecticut Agricultural Experiment Station. It seems probable that East's (1908) first paper on inbreeding in corn was completed after reading Shull's manuscript on the same subject; however, East's paper was published prior to that of Shull. East's studies with Love at Illinois, as described by Crabb and by Jones, show that East was interested in the effects of inbreeding corn before the time of Shull's first work in this field.

East and the writer carried on studies similar to those of Shull of crosses between inbred lines that gave marked superi-

Figure 6 Inbreds and F_1 crosses grown at the Connecticut Agricultural Experiment Station in 1911. The two rows at the left are inbred lines of Leaming Dent selfed for five generations. Those at the right are F_1 crosses of these inbreds. The writer stands in the center of the photograph. Dr. East made one of his characteristic statements on a three-day visit to Connecticut from the Bussey Institution of Applied Biology, Harvard University. He said, "This material would create a sensation if grown in the Corn Belt." (After East and Hayes, 1912)

ority over open-pollinated corn varieties, but we did not see how these crosses could be used commercially. This led to a restatement of the desirability of variety crosses by Hayes and East (1911), and data on varietal-inbred crosses were included with those from varietal crosses. The viewpoint of East on the desirability of varietal crosses was similar to that of earlier workers. A summary of varietal crosses will be given in a separate section.

The studies at the Connecticut Station were continued after Shull became interested in other than corn genetic research. These Connecticut studies included both breeding and genetic researches.

The genetic studies provided results presented in several papers. Two major publications on inheritance entitled, "Inheritance in Maize," by East and Hayes (1911) and "Further Experiments on Inheritance in Maize," by Hayes and East (1915)

presented the greater part of the inheritance studies.

The data on aleurone color, used by the writer for a special problem in genetics as a part of graduate work at Harvard, and the data on inheritance of endosperm color and of size inheritance used by East in his 1910 paper on the Mendelian inheritance of quantitative characters are given in detail in the 1911 publication. The aleurone studies showed that several genetic factors interacted to produce the various types of aleurone color. The placing of size inheritance on a Mendelian basis was an important step in the development of the idea that many important characters of plants are inherited in a Mendelian manner.

When East (1910) gave this paper to Castle to read before publication, Castle told East of a publication of Nilsson-Ehle (1909) published the previous year in which a similar viewpoint was expressed. Nilsson-Ehle, therefore, received credit for the idea, although it was independently discovered by Dr. East. Subsequent knowledge that common wheat is a hexaploid with three basic chromosome sets or genomes, leads to the conclusion that Nilsson-Ehle's multiple factors for grain color are located in different genomes. Studies of the writer of the inheritance of leaf number in tobacco (1912), and the many studies of Dr. East and others were of value in calling to the attention of students of quantitative inheritance the complex manner of inheritance, even though of a Mendelian nature, of this class of characters.

Reference to a further paper on quantitative inheritance in maize seems worthwhile. This was published in 1913 by Emerson and East in Nebraska Agricultural Experiment Station Research Bulletin 2. This paper included much of the work carried out prior to that time by both writers. The discussion of methods of breeding for quantitative characters is without doubt the most complete and desirable statement made in this early period on this subject.

The 1915 bulletin by Hayes and East on crosses between the major groups of corn especially featured the inheritance of flinty-floury endosperm. The endosperm results from a combination of two female nuclei with a second male reproductive cell called double fertilization. Thus the endosperm tissues of corn contain n = 30 chromosomes. Segregation on the ears of F_1 plants for flinty vs. floury endosperm was on a 1:1 basis. Two doses of the flinty factor, *Fl Fl,* with one dose of floury, *fl,* produced flinty endosperm while two doses of floury and one of flinty, *fl fl Fl,* gave floury endosperm. Some information

Figure 7 The late Dr. E. M. East, who for many years was a leader in Plant Genetics and in the application of Genetics to Plant Breeding. Photograph presented by Dr. East to the writer about 1918.

was given also on the complexity of inheritance in crosses between the dent and flint groups.

The publication of East and Hayes (1912) entitled, "Heterozygosis in Evolution and in Plant Breeding," together with the later classical publication of East and Jones (1919), "Inbreeding and Outbreeding," summarized general results of studies of heterosis and the effects of inbreeding and cross-breeding in both self- and cross-pollinated plants. It may be of historical interest that East previously outlined his idea of publishing a summary of studies on inbreeding and outbreeding with me when sufficient data were available. Many examples were given by East and Jones, with both groups of plants, of the effects of heterosis. The bulletin by East and Hayes is the most complete early statement of the utilization of hybrid vigor, with various crop plants, as a means of increasing productivity.

Chapter 3 OTHER EARLY INVESTIGATIONS RELATING TO HYBRID VIGOR IN CORN

Nineteenth Century Studies of Self- and Cross-Pollination

Most discoveries such as the value of hybrid corn are developed through the combined studies of many investigators. In retrospect it appears that most of the principles now applied to the production of hybrid corn were known prior to the rediscovery of Mendel's Laws in 1900.

Thus Beal (1878), from studies started the previous year, suggested the use of F_1 varietal crosses. McCluer (1892), a horticulturist, at Illinois, studied extensive crosses between corn varieties, both in the F_1 and F_2 generations, and compared these with their parents. He wrote, "Nearly all of the corn grown a second year from the crosses is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties."

He found no sure method of predicting which crosses would give the best results. In crosses between sweet corn varieties, which he considered to be closely related, little increase was obtained by crossing. We now know (East, 1909a), however, that sweet corn varieties may be of different origins, some being of flint type and others of dent type, where the ability to produce normal starch grains has been lost. It is evident, therefore, that sweet corn varieties are not necessarily as closely related as McCluer hypothesized. In a cross between two pop corn varieties a great increase in vigor was obtained.

Illustrations of McCluer's results are presented in Table 3. His results were based on weight per ten ears. This was the method used to determine comparative yielding ability.

Table 3 Yields in ounces of 10 ears of parent varieties and their F_1 and F_2 crosses

Varieties	Parents			Crosses	
	A	B	Av.	F_1	F_2
Queens Golden (Dent) x Black Mexican (Sweet)	36	34.5	35.25	47.5	43.5
Leaming (Dent) x Triumph (Dent)	87.5	46.5	67	83	81
Queens Golden (Pop) x Common Pearl (Pop)	34.5	27.5	31	42	Not tested

McCluer emphasized the fact that the more desirable crosses could be obtained only by actual trials.

Morrow and Gardner (1892) in Illinois outlined methods of producing F_1 varietal crosses with field corn and presented data to show the value of this method of hybrid seed production.

The review by Conway Zirkle (1952) entitled, "Early Ideas on Inbreeding and Crossbreeding," discussed the studies prior to the present century, several of these being in the eighteenth century. He cited the book by Charles Darwin (1876) on, "Cross- and Self-Fertilization in the Vegetable Kingdom," which was a report by that great naturalist of his early experiments, and quoted a statement from the last chapter. Darwin wrote, "The first and most important conclusion which may be drawn from the observations given in this volume, is that cross-fertilization is generally beneficial and self-fertilization injurious."

Zirkle concluded his paper with seven summary statements of a knowledge of hybrid vigor at the beginning of the twentieth century. These included most of the facts discovered later and presented in greater detail by Shull and East. It seems evident today, however, that without the studies of East and Shull in the present century the development of the heterosis concept would have been long delayed.

Relation Between Ear-Type Selection and Yield

Before the advent of controlled methods of corn breeding, numerous studies were made of the relation between ear charac-

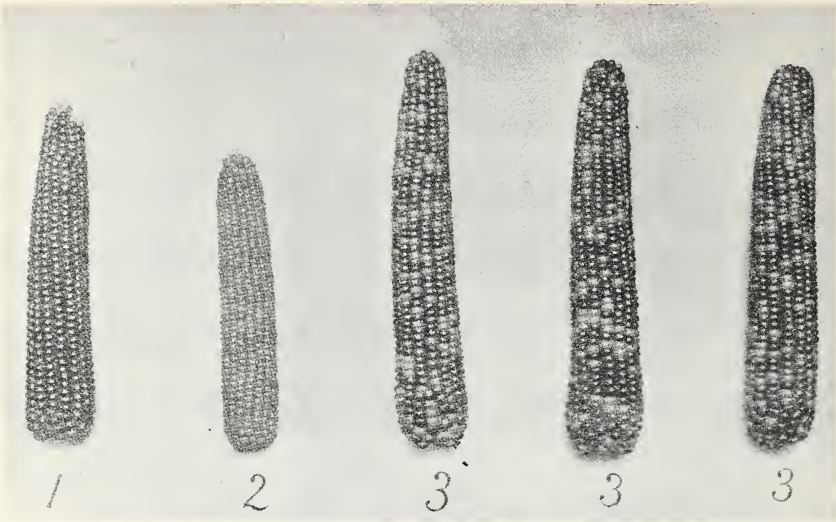


Figure 8 From the left of the photograph, ear 1, representative ear of Queens Golden Pop; ear 2, representative ear of Common Pearl Pop. The three ears, marked 3, are representative ears of the F_1 cross between Queens Golden x Common Pearl. (From McCluer, 1892)

ters and yielding ability under conditions of normal pollination. In general the well-known experiments of Williams and Welton (1915), and many others, showed no close relationship between ear characters and yielding ability. Extension workers, however, emphasized the value of selection for desirable type of ears, with well filled tips and butts. Corn Shows, also, helped to emphasize the importance of show type appearance of ears. This led to the rather general belief that continued selection for such characters would lead to corn improvement and these ideas appeared reasonable. Richey (1922) reviewed the literature on early methods of corn breeding and on varietal crosses. A brief summary of varietal crosses will be given later.

Simple mass selection for adaptation to wide differences in environmental conditions has led to the production of many different varieties and strains. Continued selection for ear type without doubt led to a form of inbreeding with consequent reduction in yielding ability. A personal incident may not be out of place.

The writer started new studies of selection in inbred lines in 1915 in Minnesota, and in these early years P. J. Olson col-

laborated in these studies. At a Farm and Home Short Course a few years later, when I explained the effects of cross- and self-fertilization in corn, the performance of F_1 crosses in comparison with open-pollinated corn varieties, and the lack of relation between show type ears and yielding ability, one of my audience became very much disturbed. He said that the value of selection for desirable ear type had been taught both in college and at extension meetings and he believed strongly in these teachings. It is probably true, however, that corn shows in these early days had real value in stimulating better methods of corn production.

One of the more interesting and illuminating studies was made by Garrison and Richey (1925) on the effect of continuous selection for ear type in Boone County white dent. Six different ear types were included in the selection, one of which consisted of show type ears, and each type of selection was carried out in an isolated seed plot. Mixed seed from at least 50 ears was used to plant each plot, and the selections were continued for an 8-year period.

The performances of various selections were compared with that from seed of the same variety without close selection to ear type. The writers concluded that all six selections were markedly reduced in yield in comparison with the normal variety. Thus, it is evident that close selection for ear type leads to a reduction in yielding ability comparable to that following inbreeding.

Nevertheless, corn growers in the early part of the present century usually practiced selection for ear type. My father, for example, in New England grew a yellow 8-rowed flint and carefully selected seed ears of uniform type, with well-filled butts and tips. Every few years he introduced seed from a nearby farmer to mix with his own seed to restore vigor to the variety.

Such selected varieties naturally would be expected to give increases in vigor when crossed with unrelated varieties. Therefore, many of the earlier studies of varietal crosses showed increased yields in F_1.

Studies of Varietal Crosses after 1900

Richey (1922), as already mentioned, reviewed the results of varietal crosses and Griffee (1922) who spoke on the same

program also gave a detail review. Hayes and Garber (1927) summarizing information on varietal crosses concluded, "Except for some special conditions it appears that varietal crosses are of no material value as a means of increasing yielding ability, provided a broad method of breeding is used by the corn breeder without close selection to type." Collins (1910) was interested primarily in basic principles of breeding and an early study that he made of varietal crosses is of interest. He introduced a considerable number of tropical varieties and 16 of the more desirable were crossed with varieties from the United States. Only about 16 hills of each were grown in comparative trials. Two hybrids yielded less than the parental average by 8 and 9 percent, respectively, two yielded more than the parental average but less than the better parent and 12 exceeded the better parent in yield. The average increase of the F_1 crosses over the parental average was 53 percent. This early study of varietal crosses emphasizes the importance of genetic diversity of parentage in its relation to hybrid vigor but this was not widely appreciated at the time. An appreciation of this fact would have been of great value to many controlled pollination studies. It was learned the hard way that it was difficult to produce a good double cross from inbreds selected from a single variety.

It is worth emphasizing again that East believed properly selected varietal crosses were of greater value as a means of utilizing hybrid vigor than single crosses between inbred lines as suggested by Shull.

In this connection it is noteworthy that varietal crosses could be made today that would perform as favorably, as far as yield and plant characters are concerned, as the double crosses now used so widely. It has been demonstrated that crosses between advanced generation single crosses yield as well, on the average, as double crosses of the same origin (Kiesselbach, 1930). Each advanced generation single cross really represents a synthetic variety, and in some cases such synthetic varieties might yield sufficiently well to be used as parents of a double cross.

Other Early Studies of Controlled Pollination Methods

It seems worthwhile to mention that Shamel at Illinois, East and Smith at the same station, and Hartley of the U. S. Department of Agriculture, who was in charge of corn investi-

gations, studied the effects of self-fertilization as a method of corn breeding prior to the later work of Shull and East. It is noteworthy that the late Perry G. Holden, an early and well-known leader in extension work, who received B. S. and M. S. degrees at Michigan State in 1889 and 1895, respectively, studied inbreeding and cross-breeding in corn in the latter part of the nineteenth century (see Richardson, 1959). These investigations were carried out at the University of Illinois when a student there before completing his undergraduate work and were not known until revealed in 1948 by Mr. Holden as a phase of hybrid corn history.

Inspired by the work of East and Shull, studies of the effects of self-fertilization were started at Nebraska in 1909 under the leadership of E. G. Montgomery. The resultant inbreds had their origin from twelve productive ear-to-row strains, five high leaf area selections and seven of low leaf area, from the standard variety, Hogue Yellow Dent.

In 1912 Montgomery moved to Cornell University, and from that time until his retirement in 1952, T. A. Kiesselbach, who started as Montgomery's assistant in 1909, was in charge of the Nebraska corn improvement program.

Third generation selfed lines were first tested in single crosses in 1913 under severe drought conditions (Kiesselbach 1922). As a four-year average (during 1913, and 1915-17), eight single cross hybrids averaged 17 per cent higher in grain yield than the original Hogue's. Unfortunately these early crosses were very susceptible to lodging. This led to the initiation of selfing of plants of Nebraska White Prize in 1914.

Commenting on the failure of these first eight years of Nebraska hybrid corn research to bring out definite recommendations for farm application, Crabb emphasized that progress in these early days came slowly, and made the completely inaccurate statement that "George Harrison Shull knocked on the door of an empty house." At this time the basic principles were still being sought, had not yet been fully understood and practical applications were not yet obtained. Kiesselbach endeavored to produce hybrids from a single variety and found this to be difficult, just as the writer and associates learned from Minnesota studies. All experienced corn breeders know that, due to the cost of seed production, it would have been impossible to influence farmers to produce single crosses as early as 1910 after Dr. Shull's pure line method was outlined. This is very evident if one examines carefully Fig. 5 where the upper row

represents the best ears from 50 plants of Dr. Shull's inbred that had the more desirable ear production.

Henry A. Wallace started studies of the effects of self-fertilization in 1913 as a private enterprise. This led eventually to the organization of the Pioneer Hi-bred Seed Company of Iowa. Wallace took part in some of the early meetings of workers in corn breeding, both in informal discussions and in the presentation of formal papers on breeding. In some instances he has been referred to as the father of hybrid corn. It is evident to this writer that hybrid corn had many fathers and that it like other outstanding accomplishments has resulted from the work of numerous investigators.

Although self-pollination and selection in corn was started in Minnesota in 1914 by Hutcheson and Olson, they used a method of selfing by means of a paper cone covering the ear and tassle which proved unsatisfactory under Minnesota conditions, where there are often rather strong winds during the period of pollination.

To keep the record straight it seems desirable to correct a statement of Crabb's (1947) in "The Hybrid Corn Makers." He wrote, "Because his colleagues at the University of Minnesota were unable to appreciate the possibilities of corn hybridization, Hayes was unable to start on corn inbreeding until 1920." Certainly this was not true. I was given a free hand to direct the breeding with corn and other farm crops. Funds were limited in the early days for breeding studies as for other Station researches. However, inbreeding with Minnesota corn varieties was begun in 1915 at University Farm. We also studied varietal crosses, the relation between ear type and yield, the inheritance of protein content using selfed lines of Minnesota #13, the inheritance of mosaic pericarp pattern through several selfed generations, and from crosses of selfed line parents. Reports of each of these studies were published prior to 1920. These studies seem to me to have an important relation to knowledge of the effects of inbreeding and the value of corn hybrids in relation to corn improvement.

F. D. Richey began self-pollination in 1916 when C. P. Hartley was in charge of the U.S.D.A. corn project. As early as 1902 Hartley and Collins had decided, on the basis of several seasons' observations, that inbreeding by self-pollination was of little value. However, Richey started selection studies in selfed lines even though he was working with Hartley. In 1922 Richey was placed in charge of corn investigations for the U. S.

Department of Agriculture and led, as will be given in greater detail later, in developing cooperation between State and Government corn breeders.

Studies of self-fertilization were started in 1916 by both C. H. Kyle and J. R. Holbert as a phase of corn improvement of the U. S. Department of Agriculture. Crabb in "The Hybrid Corn Makers" described the early interest of Holbert in corn improvement from his college days through the years when he worked at the Illinois Station and his later studies at the Federal Field Station on the farms of the Funk Brothers' Seed Company near Bloomington, Illinois. He also outlined his work as a leader of the Funk Brothers' corn breeding program. Crabb described the first summer after Holbert graduated from Purdue when he was engaged in a cereal disease survey in Minnesota. His corn breeding work was started after Holbert visited the writer in August, 1915, and Holbert gives credit to him for emphasizing the probable ultimate importance of breeding corn by selection in self-pollinated lines and the eventual use of these lines in hybrid combination. The writer remembered this discussion with Holbert but until Crabb's book appeared did not have much appreciation of the extent of this influence.

Holbert carried on corn breeding at the Federal Field Station for many years. In 1921 I visited this station and was impressed with the extent of work and the desirable inbred material that Holbert was developing. I arranged a few years later to obtain a few of the more promising inbreds from Holbert which I thought might be adapted for use in southern Minnesota. Although never used directly in hybrids certain of these "H" lines proved valuable parents in crosses from which improved inbreds were obtained.

Crabb emphasizes the work of Holbert from the standpoint of resistances to corn diseases including smut, ear and stalk rots. It is only natural that differences in disease reaction of inbreds would be observed at this station, set-up partially at least to study corn diseases. Such differences as Holbert observed were being found also at this time in all field laboratories where selection in selfed lines was being practiced. However, one should credit Holbert with many studies of disease and insect resistances, as well as of resistance to frost injury. Many of these studies have been in cooperation with other investigators who were research leaders in their chosen fields. Holbert's early inbreds which he shared with others were of great value in these early days.

Among other early studies of selection in self-pollinated lines and their use in hybrids the work of Dr. G. N. Hoffer and associates at Purdue University, Lafayette, Indiana, deserves special comment. These investigations were started in the Purdue Botany Department in 1917, primarily to study the root rots of corn. The reactions of individual plants were so highly variable that when Burr-Leaming became available, seed was obtained from Jones in 1919. The results with this hybrid were more uniform. This led to selection in selfed lines of Reid's Yellow Dent, starting in 1920 when 1500 selfed ears were produced. Hoffer and associates emphasized inherited differences in reaction to root rot in relation to inherited differences in nutritional requirements. Hoffer also emphasized the importance of selecting under conditions of low productivity.

Approximately 600 samples of hybrid corn were distributed for testing by Purdue Agricultural Alumni in 1927, and ten ear samples of the results were demonstrated at Purdue in January, 1928.

Merle T. Jenkins started as an assistant of C. P. Hartley in 1919 and visited the writer that fall. Jenkins also credits the writer with interesting him in the newer method of corn breeding which led him to start self-fertilization the following year. He has emphasized also the writer's appreciation in 1919 of Richey's capabilities of stimulating research leadership in corn breeding. During 1921 Jenkins spent the year with Holbert at the Federal Field Station located on the Funk Farms. Later work of Jenkins will be discussed in relation to special phases of corn breeding.

Early Cooperation in Corn Breeding

In the early twenties Richey led in arranging conferences between State and Federal corn breeders in the Corn Belt. These early conferences were attended in part by Wallace. The value of such conferences both in the field and laboratory was evident to all workers. Corn improvement a few years later in 1925 was placed on a cooperative basis by the Corn Belt State Stations and the U. S. Department of Agriculture under thePurnell Act, and an appointed committee consisting largely of research workers, formulated a cooperative program. This program was set up so that the initiative of individual workers was not suppressed.

Annual meetings, sometimes in the field and in other years in the laboratory, were continued for several years. The exchange of materials and ideas were fostered by these frequent meetings. Inbreds from various corn breeding programs were grown and observed at other research stations. Even though the double-cross method was well known, the difficulties to be surmounted still appeared rather troublesome. A catch phrase at these meetings was frequently discussed. It was as follows, "Now that we have got them what are we going to do with them?" referring to the rather large group of inbred lines available and the difficulties of finding the better double crosses for the many different environmental conditions under which they would be grown. The ideas of Richey, Stadler from Missouri, and Lindstrom from Iowa, were very stimulating to members of these corn conferences.

Several early ideas are remembered by the writer as expressed by these men. At one meeting Richey presented data to show that some inbreds tended to give high yields in nearly all crosses with other inbreds, while other inbreds gave less uniform performance in crosses (See Richey, 1924, Richey and Mayer, 1925). This seems one of the outstanding early conclusions relating to a knowledge of combining ability.

Stadler emphasized the importance of retaining a broad source of germ plasm, and this led to a combined effort to retain material of the more valuable open-pollinated varieties in each state and region. Important open-pollinated varieties are being maintained today at the various cooperating Stations in the Corn Belt. In this connection the writer joins with Henry Wallace in emphasizing the importance of the work of Dr. Paul Mangelsdorf, who incidentally was a student of Dr. East, in leading in the arrangements, under the auspices of the Rockefeller Foundation and the National Research Council, to maintain a collection of different corn strains of Mexican and South American origin for future use of students of corn breeding and of corn genetics. Dr. Stadler should share in credit for the idea as he initiated the movement to maintain important strains of Corn Belt varieties.

Lindstrom emphasized the probable importance of maintaining a considerable degree of heterozygosity without too rapid approach to homozygosis, so that selection could be practiced over a somewhat longer period than is usually the case when continued self-pollination is followed in selecting and producing inbred lines. This seems to the writer to have considerable

Figure 9 Photograph of the late Dr. F. D. Richey who led in cooperative investigations and who made many very valuable contributions to corn breeding methodologies.

relation to the present-day method of breeding by recurrent selection. Sib-pollination within an inbred line furnishes an opportunity to practice a type of visual selection and to obtain new and better combinations of genes that are carried by the line.

These are the more important suggestions that were made in the light of present day knowledge. There were many other ideas presented and discussed that seem of somewhat less importance. The free exchange of ideas and materials without doubt was responsible to a large extent for the progress in hybrid corn breeding and the wide acceptance of hybrid corn throughout the Corn Belt.

Chapter 4 TWO IMPORTANT CONTRIBUTIONS OF JONES

Introduction

As stated previously, Jones continued the investigations first started by East in 1905 and carried out by the writer through 1914. During the early years of Jones' researches, he spent the winter months at the Bussey Institute in graduate work with Dr. East as his major adviser. His Ph. D. thesis (1918) was a continuation of investigations on inbreeding and cross-breeding in corn. Jones' major early contributions were two-fold.

The Double-Cross Plan

One of these, the double-cross plan, as suggested by Jones (1918, 1919) used seed of a cross between two single crosses as the commercial crop. Two of the inbreds in the most desirable double cross, Burr x Leaming, were from East's first selfed lines of Leaming. The two Burr inbreds were selfed lines of the Burr variety obtained when the writer, at East's suggestion, initiated a study of the inheritance of protein content. Double crosses are the major source of seed used by the commercial producers of corn, although 3-way crosses and single crosses are grown also but not so extensively. This double-cross plan, which made commercial seed production not too costly, was responsible also for an increase in the support of controlled pollination methods of corn breeding.

The value of the plan as a basis for obtaining more adequate financial support for basic studies of corn breeding may be illustrated in its effect on the corn breeding program at Min-

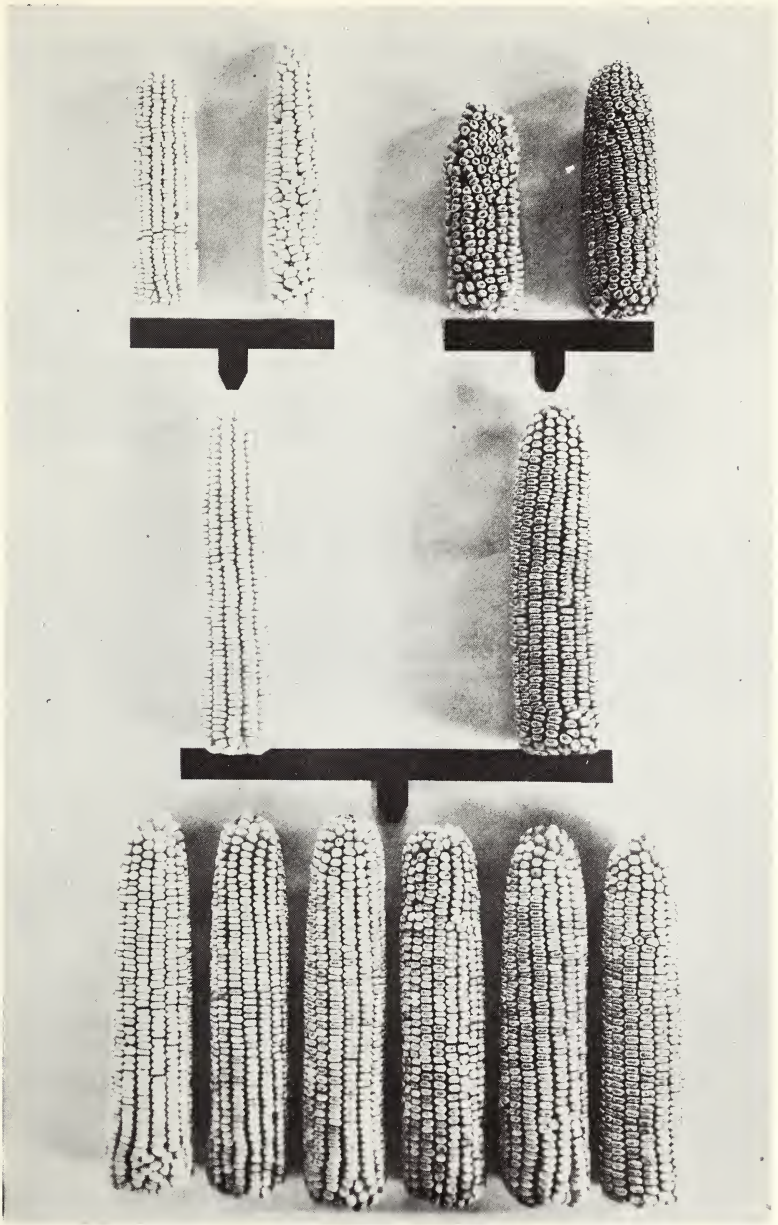


Figure 10 Burr-Leaming, the first double-cross hybrid produced commercially. Upper row, at left, inbreds of Burr White; at right, inbreds of Leaming. Central row, at left, Burr single cross; at right, Leaming single cross. Lower row, representative ears of the commercial crop (Photograph furnished by D. F. Jones)

nesota. Although the writer started new experiments at Minnesota in 1915 on controlled self- and cross-pollination in corn, the available financial support was not as extensive as seemed desirable. When Andrew Boss, Chief of the Division of Agronomy and Farm Management at University Farm, St. Paul, read about the double-cross plan, as given by Jones (1919) in the Breeders Gazette, he immediately brought it to the writer's office and said about as follows: "This makes hybrid corn feasible; we must find more support for your work." In 1920 a rather extensive corn breeding program was started at the Southern Experiment Station in Waseca, Minnesota, in addition to increased aid for the studies at University Farm. It is very evident that other breeding programs with corn were given greater support at about this same period.

A Mendelian Explanation of Hybrid Vigor

Jones' second contribution (1917) was to place heterosis on a Mendelian basis by an explanation called dominance of linked growth factors. This renewed the hypothesis of Keeble and Pellew (1910), and Bruce (1910), and added the phenomenon of linkage. It seems evident that linkage does add to the difficulty of combining the favorable factors of the parents of a cross, in a homozygous condition in selfed progenies. The fact that all selfed lines from crosses were less vigorous in F_2 than in F_1, seems to have been the main reason why Shull, East, and others, at this early period, did not consider that heterosis could be placed on a Mendelian basis. With only a few factors involved in a cross, and with dominance, the curve of variability in F_2 would be skewed. However, the F_2 curves that were studied approached the normal. Collins (1921) showed, however, that if many factors were responsible for the expression of a quantitative character, large numbers of individuals would need to be studied in F_2 to obtain much of a departure from the normal curve regardless of whether linkage or independent inheritance was the rule.

Although Keeble and Pellew (1910) explained hybrid vigor in the pea cross that they studied on a di-hybrid basis, Bruce (1910), as has been emphasized by Richey (1945a), used the dominance hypothesis for her explanation, but in the mathematical presentation hypothesized that numerous genes were concerned in the expression of hybrid vigor. Therefore, the writer

agrees with Richey that Bruce deserves major credit for the Mendelian explanation, although a knowledge of linkage was not available at this time. When it was appreciated that many normal characters are dependent for their expression on rather large numbers of factors, as seems to be the case usually for heterosis, linkage of some of these factors follows naturally. Here, as in other cases of like nature, Jones' explanation was timely, and therefore the hypothesis of dominance of linked factors, as outlined by Jones, stimulated further studies of the causes and utilization of heterosis.

Selection in Selfed Lines

At about the same time Jones (1920) wrote a paper entitled, "Selection in Self-fertilized Lines as a Basis of Corn Improvement." It seems probable that Jones thought that this was a new idea. When Jones was a visitor in my home some years ago, I gained the impression that he thought East, Shull, and the writer failed to select during the period of self-pollination. I told him this was a new idea to me, as individual plant selection was the primary tool of the plant breeder during the early years of the present century. I also outlined my idea that the breeding of selfed lines of corn seemed to me to be carried out in the same way as the breeding of new varieties of self-pollinated plants such as wheat. Even though many corn breeders in 1920 were practicing selection in self-pollinated lines as a basis for their later utilization in hybrids, it was evident that Jones thought he did not receive the credit due him for this study. Finally I said that perhaps his major difficulty in this case was a lack of appreciation of the extensive studies under way, even in 1920, in the Corn Belt. We agree, however, that the terminology, selection in self-fertilized lines, was first used by Jones, although the methods certainly were not first discovered by Jones.

While a later proposal of Jones and Singleton (1935) was made after there were numerous valuable additions to controlled pollination methodologies, as applied to corn, it fits well into the story at this time. As with breeding small grains, selection in the early segregating generations of corn inbred lines has been largely on the basis of visual characters, and studies of actual yield are difficult to carry out with large numbers. Each plot of self-pollinated lines of corn usually has consisted of 20

to 30 plants, and rather large areas of land are needed when large numbers of corn inbred lines are grown. It is usually thought that selection between lines is more important than selection within lines. Jones and Singleton's suggestion was to grow only a single three- or four-plant hill of each line, thus making it possible to grow several thousand inbred lines per acre. This method has been used rather extensively in Minnesota, during the early generations of selection in selfed lines when many lines usually are discarded, by growing, for each inbred line, a short row of four plants each, with plants separated by 12 inches in the row. After several generations, the remaining lines then are grown in 12- to 20-plant plots to facilitate selection of lines for first studies of combining ability.

Chapter 5

THE RELATION OF CHARACTERS OF INBREDS TO THOSE OF THEIR HYBRIDS

Introduction

During the early years of selection in selfed lines the more desirable plants usually are selected and selfed. Final selection is made as the lines approach homozygosis, by selection between lines although this method is used also during the early years of inbreeding. After the inbred lines become relatively uniform, often after 4 or 5 years of selfing, the relative desirability as inbreds can be determined by a comparative study of important characters in replication studies of the inbreds under trial. Tests in different seasons, and localities, also aid in inbred evaluation. That the characters of inbreds become fixed by selection and inbreeding is axiomatic according to present day viewpoint. It also is appreciated that inbred lines are more responsive than single or double crosses to variations in environmental conditions.

Jones and Mangelsdorf (1925) found little relation between characters of inbreds in the first and sixth generations of selfing where selection in selfed lines had been carried out. In another experiment in the first generation of selfing they separated selfed lines into upper and lower halves on the basis of plant height, percent of moldy ears, number of tillers per plant, percent of plants with smut (in the second generation) and yield of grain. They compared the characteristics of the lines in this early generation with those of the same lines after 4 or 5 generations of selection and selfing. They wrote, "It will be seen that the relative position of the upper and lower halves remains nearly the same at the end of the period of selection as at the beginning."

This did not hold, however, for yield of grain where both halves yielded about the same at the end of the selection period.

Hayes (1926) presented a rather extensive series of studies of characters as expressed in different generations of selfing. Each trial, however, consisted of only a 20-plant row. The comparisons were made by correlation studies. The conclusion was as follows, "In general the larger coefficients were obtained for length of ear, size of seed and cob discoloration," also, in some cases percentage of lodging and smut infection. Yielding ability of inbred lines in different selfed generations gave a positive correlation in most cases.

Richey and Mayer (1925) wrote, "The data indicate, however, that there is little or no relation between the productiveness of the self-fertilized lines and that of their crosses and that the final value of the lines for crossing must be determined by comparison of the productiveness of their crosses."

The results to be presented later show very definitely that with a representative group of unrelated inbred lines adapted to a locality there is usually a positive and important relation between the overall vigor of selfed lines and the yielding ability of their crosses. It has been generally accepted by corn breeders that the final value and utilization of inbred lines can be determined only by studying their crosses.

However, the extent to which there is a positive relation of the characters of inbreds and their average performance in single crosses is of considerable interest.

Correlation Between Characters of Inbreds and their Hybrids

An early study of the relation between the characters of inbred lines and of their single crosses was carried out by Nilsson-Leissner (1927) as a phase of post-doctorate studies at Minnesota under the supervision of the writer.

The inbred lines included 14 strains of dent varieties, 4 from Minnesota #13, 6 from Rustler and 4 from Northwestern dent; and 9 strains of flint varieties, 4 from Longfellow, 2 from King Philip, 2 from Squaw and 1 from a Red Flint. Two of the inbreds had been selfed for 4 years, 1 for five years, 4 for six years, 11 for seven years, 2 for eight years, and 1 each for eleven and seventeen years, respectively. These inbreds were the more promising inbreds available at this time from the University Farm program.

Two replications of 15 hills per plot were grown, and yields and other characters were taken on two or three stalk hills surrounded by corn on four sides. Border rows as necessary were used to eliminate competition between materials which were widely different in performance.

Nilsson-Leissner compared the performance of inbreds and sib-pollinated strains of the same origin when grown in adjacent rows with two replications, using Student's method (1908). The characters studied included height of plant, length of ear, ear diameter, ear row-number, percentage of second ears per stalk, and yield on a grams per hill basis. There were no cases of great differences between the inbreds and their sib-pollinated relatives, indicating that the inbreds were relatively homozygous.

Simple correlations were calculated in the flint and dent groups, respectively, for interrelations of yield of F_1 crosses and the average performance of the inbreds for yield, length of ear, number of kernel rows, percentage of second ears, and height of plant. All were positive and significant except the correlation in the dents of average percentage of second ears and yield of the F_1 crosses. The multiple correlations of yield of F_1 crosses with the average performance of the parent inbreds for yield, length of ear, number of kernel rows, percentage of second ears, and height of plant were +.67 in the dents and +.82 in the flints. These results gave considerable support for the belief that the vigor of inbreds has a positive and important relation to the yield of their F_1 crosses.

Jorgensen and Brewbaker (1927) made a similar study to that of Nilsson-Leissner, using 10 selfed strains of Silver King, 3 of which had been selfed for three years, and the others for four years. These 10 inbreds were selected from 250 available inbreds. They excelled in freedom from abnormalities and were among the most vigorous and promising inbreds available from this material.

The inbreds were compared with sib- and self-pollinated material, 16 hills per plot being used when seed was available. Sib-pollinated material of the same line were grown in adjacent rows, bordered on the sides by normal Silver King, with three replications. Yields and other characters were studied from two or three stalk hills surrounded on four sides by two or three stalk hills. The data taken included yield of grain per hill in grams, weight of cob, height of stalk, length and diameter of ear, number of ear-rows, percentage of second ears, percentage of

suckers, percentage of moldy ears, and percentage of smut infection. Odds were calculated by Student's Method to determine if there were differences between sib-pollinated and self-pollinated progenies for the ten inbreds. There was little or no evidence of a consistent superiority of sib-pollinated over self-pollinated. This does not show whether there were significant differences in individual lines, although there were about as many cases in which the selfed line exceeded the sibbed line as vice versa.

Thirty-seven of the possible 45 hybrids were studied in replicated field trials. Yields of single crosses were correlated with the averages of their parental inbred lines for yield, length of ear, diameter of ear, number of kernel rows, and height of plant. The simple correlation coefficients ranged from 0.48 to 0.79 and all r values were positive. A multiple R value of 0.61 was computed for the yield of F_1 crosses and the above characters of the inbreds. While it is apparent that actual trials were necessary to determine the better crosses, the positive relation between characters of the inbreds that are expressions of growth vigor and their performance in hybrids is evident.

Jenkins (1929), in Iowa, published an extensive study of the relationship of characters of inbred lines and their behavior in hybrids. The details of the study can be appreciated only by a study of the data.

There were 80 inbreds in the study, 5 obtained from Holbert, 1 from Lindstrom, the remainder were developed by Jenkins from various varieties representing a rather wide diversity of germ plasm. There were 20 inbreds in Group 1 of white endosperm corn; each of the inbreds 1 to 10, except 8 were crossed with inbreds 11 to 20 inclusive, making 90 hybrids. In Group 2, consisting of early maturing inbreds of yellow endosperm corn, each of the inbreds 21 to 30, except 23, were crossed with lines 31 to 40, making 90 hybrids. In Group 3, 10 of the lines were selected, and as far as possible each of these was crossed with the other 29.

The data on inbred parent lines used in the correlation studies were taken in 1926 when the lines had been selfed for four years, while data for the crosses were taken in both 1926 and 1927. As the 1927 data were less extensive, they have not been included in this review. Richey's moving average method was used to correct for soil heterogeneity.

Because of the methods used in the study it was possible

to correlate the average yield of each parental inbred with the average of several F_1 crosses.

The r values for yield of inbreds and the average yields of their single-cross progenies, were in the three groups; .67 ±.09, .64 ± .09, and .25 ± 14, respectively. Jenkins concluded, "Some inbred lines produced high-yielding crosses in practically all combinations. Other lines produced some high-yielding crosses and some low-yielding crosses. Still other lines produced crosses practically all of which were low yielding." Nevertheless Jenkins found a significant and important relation between the characters that represent vigor in the inbred lines and the average performance for yield and other characters in their F_1 crosses.

Hayes and Johnson (1939) reported an extensive study of the relation of characters of inbred lines and their combining ability in inbred-variety crosses using Minnesota #13 as the open-pollinated parent of the crosses. The inbreds included 6 parental inbreds that had been used previously in crosses for the purpose of producing improved inbreds combining the desirable characters of both parents, 86 inbreds that were selected from these crosses after six years of self-pollination, 13 inbreds from open-pollinated varieties, and 4 inbreds from Wisconsin.

The 110 inbred lines were grown in randomized blocks at University Farm for three seasons, using row plots with 25 single-plant hills, spaced one foot apart and two replications each season. Yield trials of the inbred-variety crosses were made using randomized blocks at three locations, University Farm, St. Paul, the Morris Branch Station, and Breckenridge, with three replications at each location. Each plot consisted of a single 12-hill row, thinned to three stalks per hill. Four check varieties were grown in each block, and the calculated yields and moisture content at husking were placed on a percentage basis, taking the average of the four check varieties as 100.

Because three-year averages were used for evaluating the inbreds, and the inbred-variety crosses were tested at three locations, individual data on each parent and cross would seem to be more reliable than often is the case in similar studies.

Inbred characters studied included date silked, plant height, ear height, leaf area, pulling resistance, root volume, stalk diameter, smut percentage, total brace roots, tassel index, pollen yield, yield index, and ear length. In inbred-variety crosses data were taken on yield, moisture percentage at husking, plant height, smut percentage, ear length, and shank length.

Correlations between the characters of inbreds and those of inbred-variety crosses not including yield are presented in Table 4.

Table 4 Correlations between Characters of 110 Inbreds and Similar Characters in their Inbred-Variety Crosses

Inbred Character	Inbred-Variety Cross Character	r
Date silked	Moisture percentage at husking	0.57*
Plant height	Plant height	0.37
Smut percentage	Smut percentage	0.46
Ear length	Ear length	0.47
Shank length	Shank length	0.54

* All r values exceeded the 1 per cent point

All five characters of the inbreds were positively and significantly correlated with comparable characters in the inbred-variety crosses.

All possible simple product moment correlation coefficients were calculated between the twelve characters of the inbreds and each of these was correlated with the yield of inbred-variety crosses (see Table 5).

It is apparent that nearly all interrelations among the characters of the inbreds were positive, and that nearly all correlation coefficients equalled or exceeded the r value for a P of .01. The exceptions were the inbred characters designated as 13, inbred yield index, and 14, inbred ear length. All twelve characters of the inbreds showed a positive correlation with the yield of inbred-variety crosses, and all except the correlation of inbred character 9, tassel index with inbred-variety yield, were as great as the calculated significant value at the 1 per cent point.

A multiple correlation was calculated between the yield of inbred-variety crosses and the twelve characters of the inbreds. The R value obtained was .67 while that for the 1 per cent point, for degrees of freedom of 100, was .47. The square of the correlation coefficient is used to determine its importance. Squaring

Table 5 Total Correlations between 12 Characters of 110 Inbreds and the Yielding Ability of Inbred-Variety Crosses

Characters of Inbreds*	Characters of Inbreds, 1 to 14 and of the F_1 Inbred-Variety Cross, 15											
	2	3	4	5	6	7	8	9	10	13	14	15
Inbred 1	.51	.61	.48	.65	.62	.55	.38	.37	.22	.07	-.06	.47
Inbred 2		.76	.44	.48	.43	.40	.26	.19	.36	.25	.08	.27
Inbred 3			.43	.54	.50	.41	.35	.33	.22	.15	.01	.41
Inbred 4				.50	.44	.48	.40	.29	.18	.20	.08	.29
Inbred 5					.76	.51	.60	.40	.21	.15	.03	.45
Inbred 6						.55	.74	.39	.29	.19	.03	.54
Inbred 7							.54	.24	.27	.21	.15	.41
Inbred 8								.26	.22	.20	.07	.45
Inbred 9									.20	-.00	-.03	.19
Inbred 10										.34	.32	.26
Inbred 13											.64	.25
Inbred 14												.28

Significant value of r for P of .05 = 0.19
Significant value of r for P of .01 = 0.25

* Key to Characters

1 Inbred date silked
2 Inbred plant height
3 Inbred ear height
4 Inbred leaf area
5 Inbred pulling resistance
6 Inbred root volume
7 Inbred stalk diameter
8 Inbred total brace roots
9 Inbred tassel index
10 Inbred pollen yield
13 Inbred yield index
14 Inbred ear length
15 Inbred-variety cross yield

.67 gives .4489 so we may conclude that 45 per cent of the squared variability in yield of the inbred-variety crosses was dependent upon the twelve characters of the inbred parents of these crosses.

It is known that usually under Minnesota conditions there is a definite positive relation between time of maturity and yield. Holding date silked constant the calculated R value for the eleven remaining characters of the inbreds and inbred-variety yields became .53. On this basis 28 per cent of the squared variability

of the inbred-variety crosses is correlated with eleven characters of the inbreds.

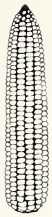
Richey (1945b) summarized studies of Jenkins and Brunson in which the yield of inbreds, and of inbred-variety crosses, were compared with the mean yields of single crosses using inbreds that had been selfed for three to six years (see Table 6).

Table 6 Coefficients of Correlation for the Yields of Inbred Parents and of Inbred-Variety Crosses with the Mean Yields of Single Crosses

Mean of Single Crosses Correlated with	Previous Generations of Inbreeding		
	S_3	S_4	S_6
Inbred parents	.25, .64, .67	.41, .45	
Inbred-variety crosses	.53	.53	.63, .65, .66, .90, .90

In these studies the yields of the inbred parents in S_3 and S_4 were about as strongly correlated with the mean yields of single crosses, as were the yields of inbred-variety crosses with the mean yields of single crosses. This serves to show in these studies that there is a rather significant relation between yields of inbreds and their average combining ability in single crosses.

Methods of breeding now being used are rather constantly leading to improved inbred lines with better combinations of characters. This when expressed as combining ability in crosses may lead to improved yields of double crosses.

Chapter 6  THE DISCOVERY OF TWO METHODS OF PREDICTION

Introduction

After the double-cross plan had solved the major part of the difficulty of making seed production of hybrid corn economically feasible, there was increased support, as has been explained previously, for hybrid corn researches. A great deal of attention then was focused on the production of good double crosses. The problems of finding the better double crosses for each environmental region, however, proved very difficult and time-consuming. Some writers have featured the slow acceptance, at first, of hybrid corn by the public without appreciating, as I think corn breeders themselves did, that a major difficulty of finding good double crosses still remained to be solved. The permutations and combinations that can be made from even a limited number of inbreds are very large, to say the least. It is no wonder, as has been pointed out previously, that the cooperative group of breeders in the North Central region discussed the problem, as exemplified by the question, "Now that we've got them, what are we going to do with them?" in reference to the inbreds.

Prediction of General Combining Ability

As has been stated there was a gradual accumulation of evidence and general acceptance among breeders of the idea that some inbreds combined well with all, or most all, other inbreds to give relatively desirable F_1 crosses. Other inbreds, equally desirable in themselves, were less reliable producers in F_1

crosses. To test, however, the relative combining value of an inbred by crossing it with a group of ten other inbreds used as testers, as suggested by Richey, required numerous yield tests for each inbred to be tested and these trials were expensive and time-consuming.

Jenkins and Brunson's (1932) study gave the clue to solution of the problem of testing inbreds for general combining ability, although the first suggestion for using comparative tests of inbred-variety crosses for this purpose was made by Davis (1929). It does not seem necessary here to give Jenkins and Brunson's results in great detail. What they studied, in a rather careful manner, was the comparative value of varieties and inbreds used as testers to determine the general combining ability of inbreds of similar maturity and origin.

In one series they compared the relative performance of selected inbreds in inbred-variety crosses and also in a series of comparable single crosses with nine to twelve other inbreds from which the results were averaged. Correlation coefficients were calculated to determine the extent of association between these two methods of testing general combining ability. There were eight different experiments and eight correlation coefficients were calculated. All eight were positive and they ranged from 0.53 to 0.90.

In another extensive series the combining ability of each inbred was determined separately from averages of single crosses from each of two different sets of inbreds. There were 3 separate studies and in each correlations were calculated to determine the extent of association between the results obtained in the two tests. All r values were positive and the three ranged from 0.62 to 0.80.

It is evident that in this study the inbred-variety crosses gave as satisfactory predictions of general combining ability as did separate tests of F_1 crosses using a series of about ten inbreds used as testers.

Johnson and Hayes (1936), a few years later, studied the comparative performance in yield trials of 11 selected inbreds of Golden Bantam sweet corn in all possible single crosses and in inbred-variety crosses with Golden Bantam and Del Maiz. The r value for yield of the averages of single crosses and the average yield of the two inbred-variety crosses was $.78 \pm .12$. These writers emphasized what has become a standard technic of many breeders. This consists of making yield trials in several locations to overcome a part, at least, of results attribut-

able to environmental variations in conditions and thus remove a part of the genotypic-environmental interactions.

Sprague and Tatum (1941) suggested using a tester that was heterozygous and that in general carried recessive factors for the character, or characters, of particular interest. Later Davis (1934) proposed using a variety as a tester that was low yielding and apparently carried recessive factors for characters of greatest interest. For any character under study such a tester could be produced by breeding methods. So far as the writer knows no such variety is available although most open-pollinated Minnesota varieties lack standing ability and the ability to yield as well as selected hybrids.

The suggestion that low yielding synthetics be used as the first tester for general combining ability merits extensive trial but cannot be used until such synthetics have been produced. There is considerable evidence to show that F_1 crosses of lines of low general combining ability as selected from inbred-variety crosses, on the average, yield much less than F_1 crosses of similar origin from parental inbreds classified as high combiners. Also F_1 crosses of High x Low yield nearly as well on the average, as F_1 crosses of High x High. The inheritance of combining ability, however, will be discussed in greater detail under a separate heading. Sprague and Federer (1951) compared the relative value of using several testers and fewer replications of each, with the use of a single tester and more replications. They concluded that an increase in the number of testers would be of greater value than increased replication using a single tester. These results will be discussed also in greater detail after the presentation of the importance of genetic diversity.

Predicting Yields of Double Crosses

There has been general acceptance of the desirability of first selection for trials in double crosses of inbreds that have high general combining ability. For characters other than combining ability much can be accomplished by visual selection of the inbreds during the process of selfing. This includes, of course, selection within and between selfed lines, in the same manner followed in breeding or selecting lines during the segregating generations in self-pollinated plants after making a cross.

After selecting the more desirable inbreds by visual means during the period of self-pollination, and the further selection of

inbreds for high general combining ability, these then are tested in three-way or double crosses. At first the method of combining lines was by the judgment of the breeder and from even a few inbred lines large numbers of different double crosses can be made.

Any four inbreds can be combined as double crosses in three different ways. Designating four inbreds as A, B, C, and D, the three possible double crosses are (A x B)(C x D), (A x C)(B x D), and (A x D)(B x C).

The usual formula for the number of different double crosses that can be made for n inbreds is

$$\frac{3n(n-1)(n-2)(n-3)}{24}$$

For 20 inbreds, 190 different single crosses can be made, and 14,535 different double crosses are possible.

Richey and Sprague (1931a) studied a method of predicting the yields of double crosses but did not obtain favorable results. Jenkins (1934) presented the first evidence in favor of the use of prediction methods. He correlated the actual yield in replicated trials of 42 double crosses with yields estimated by four methods of prediction. The methods used were as follows:

1. Using the average of six single crosses that can be made from each of four inbreds. Thus, for inbreds, A, B, C, and D, the predicted yield of the three different double crosses would be the average of the single crosses, A x B, A x C, A x D, B x C, B x D, and C x D.
2. Using the average yield of four single crosses, excluding the two used as parents of the double cross. This for double cross (A x B)(Cx D) would be the average yield of the four single crosses, A x C, A x D, B x C, and B x D.
3. Using the average yielding ability of the inbreds in all possible single crosses. Thus for 11 inbreds each could be tested in ten F_1 crosses with other inbreds, and an average yield of crosses of each of the four inbreds computed. The predicted yield of the double cross (A x B)(C x D) then would be the average of the mean yield of each of the four inbreds in ten different single crosses.
4. Using the average yields of the four possible inbred-variety crosses involving the four inbreds as an estimate of the yield of their double cross.

The r values comparing predicted with actual yields for the four methods were: Method 1, .75; Method 2, .76; Method 3, .73; and Method 4, .61 with a significant value at the 5 per

cent point of .39. Three of the methods gave practically the same value. The prediction for Method 4 was based on fewer yield trials than the other three. In discussing Method 2, Jenkins stated, "In any double cross the genes of each of the four inbreds are united with the allelomorphs of the two lines which entered the double cross from the opposite parent."

It was generally appreciated that a reliable prediction method would greatly accelerate the testing of double crosses, but at first no one appreciated the high reliability of Method 2. Thus, E. G. Anderson in discussing the method with F. R. Immer stated his belief that the method probably would not be highly accurate. The writer remembers a discussion with Richey after further tests of Method 2 had been made in Minnesota. Richey said that he supposed the method would be reliable to differentiate between the three possible double crosses that can be made with four inbreds but did not believe it would be reliable as a means of comparing distinctly different double crosses.

It seems probable that many breeders may have tested the reliability of the method independently. Extensive published comparisons of the performance of actual double crosses with predictions have been made by Doxtator and Johnson (1936), Anderson (1938), and by Hayes et al. (1943). In the latter study the yields of eight double crosses were compared with predicted yields where the trials were conducted at four locations with five replications per location. The actual and predicted yields were compared statistically in this study. There were several cases of highly significant differences between actual and predicted yields. From the practical standpoint, however, the differences were very small, and in each of the three reported Minnesota studies the differences between actual and predicted yields, using Method 2 as given by Jenkins, were of no great practical significance.

In many cases inbred lines of very similar maturity were selected for use in double crosses because this made the production of crossed seed easier since both single cross parents can be planted at the same time. If they differ slightly in maturity the difference can be taken care of by differential application of fertilizer to one or the other of the single-cross parents. In some cases, however, single-cross parents with rather wide differences in time of maturity have been used to produce desirably performing double crosses, and in these cases the parents are planted at different dates, so that both reach the pol-

lination stage at the same time. Early in the use of such double crosses in which two inbreds were classed as much earlier in maturity than the other two, it was thought best to make the cross (E x E)(L x L), using E for early and L for late. The writer remembers a discussion with Clarence Bush, of the Northrup King Company, who for many years was in charge of their breeding program. Clarence insisted that the cross of (E x L)(E x L) produced about as uniform double cross as the combination (E x E)(L x L). His conclusion was reached on the basis of rather extensive observations. At that time the writer thought that the combination (E x E)(L x L) should give the more uniform double of the two possible types of combinations.

Eckhardt and Bryan (1940a, b) studied this problem by using two early inbreds designated as E, and two later maturing inbreds designated L, where the E inbreds were from one variety and the L inbreds were from a second variety. They obtained somewhat greater uniformity for silking date, ear height, ear weight, ear diameter, and ear length for the double cross (E x E)(L x L) than for (E x L)(E x L), although the differences were not very great. Pinnell (1943) made similar comparisons crossing inbreds completely unrelated and combining them in double crosses in such a manner that two of the inbreds were classified as widely different from the other two for such characters as long vs. short ear, ear height, and time of maturity. Pinnell's results led to the conclusion that differences obtained were of little significance. Hayes et al. (1946a) made a somewhat similar study but in this case compared the uniformity of double crosses on the basis of the extent of variability among the four single crosses, A x C, A x D, B x C, B x D, used in the double cross (A x B)(C x D). While there was a slight tendency for greater variability of the double cross when the four singles differed widely, the difference was of little or no practical significance.

Jones and Everett (1949) have suggested classification of parent lines into male and female groups and making restricted combinations between these groups as a basis for prediction of performances of double crosses. This often seems desirable when two groups of inbreds are of such diverse origin that the combination of genes from the groups has the probability of giving the more satisfactory hybrids. This makes it possible to produce and test fewer single crosses since it is unnecessary to test all possible combinations of inbreds. This method often

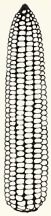
Figure 11

Crossing plot at University Farm, St. Paul, Minnesota, for the production of top-crossed seed to use in a first test for general combining ability. The desirable, high-yielding open-pollinated variety, the Morris Station selection of Minnesota #13 is used as the male parent.

Most of the inbreds in the trials are from some method of breeding, to produce improved inbreds, from crosses of desirable Minnesota inbreds with introduced inbreds from other breeders. Visual selection has been practiced and these inbreds are in S_4, fourth selfed generation. A considerable number of the inbreds have been selected under manual infestation conditions for resistance to first brood corn borers. Each inbred is planted in two short rows used to study inbred performance. The male parent variety has been planted at two dates to produce pollen over as long a period as needed. (Courtesy Minnesota Agricultural Experiment Station)

is used when two or more diverse origins are maintained, during the process of breeding improved inbred lines, with the expectation of using inbreds from one group to produce single-cross parents to cross with single crosses of inbreds of another group of different origin.

Chapter 7 GENETIC DIVERSITY



Introduction

While corn breeders have gradually come to appreciate the importance of differences in origin, or genetic relationship, in relation to general and specific combining ability, early information for the most part was obtained by trial and error methods. McCluer in 1892 emphasized the hybrid vigor of certain varietal crosses in pop corn and noted the fact that his sweet corn variety crosses gave no great increase in performance over the parental varieties. This was attributed to a closer genetic relation among sweet corn varieties than in the pop corn varieties used in the study. Collins in 1910 obtained substantial increases in F_1 varietal crosses over the parental average, or over the better parent, in a series of crosses of introduced tropical varieties with American varieties. Several studies of varietal crosses that yielded well have been reported between varieties of flint, dent, and flour corns. When double crosses were made in Minnesota using inbreds of a single variety no double cross of sufficient promise was obtained that seemed worth increasing. At the Kentucky Agricultural Experiment Station the first double cross, released in 1935, was a white endosperm hybrid, designated as double 69 (Ky 39 x Ky 21)(Ky 27 x Ky 30), where each of the inbreds was isolated by Professor E. J. Kinney from the variety, Boone County White. [1]

Since the original presentation of the story the writer has been informed of further cases where double-cross hybrids involving inbreds of a single variety have bee ı successful. Thus

[1]From personal correspondence with Frank A. Loeffel.

six or more hybrids of Neal Paymaster inbreds only were released for production in Tennessee under certification in 1938. Several of these hybrids were grown for more than fifteen years, and during 1946 to 1950 they were grown on more than half a million acres annually. In later years they have been replaced by hybrids in which the two best Paymaster inbreds are used as one parent and lines from other origins as the other parent.

The writer has not attempted to emphasize the importance and value of particular inbreds or double-cross hybrids but rather to emphasize what he considered as basic principles. Perhaps in this respect it may be interesting to utilize information received from a reader of this story in manuscript form. He emphasized the value of double crosses involving inbreds of Reid on one side of the double cross and an inbred of at least one line of Lancaster Sure Crop used in the other single cross parent.

Experimental Demonstrations of the Value of Genetic Diversity

In the studies made by Nilsson-Leissner (1927), already discussed from the standpoint of relationship between the characters of inbreds and their F_1 crosses, inbreds originating from different varieties were used. There were two different groups. The dent inbreds included three from Minn. #13, six from Rustler White dent, and four from Northwestern dent. The inbred strains of flint varieties consisted of four from Longfellow, two from King Philip, two from Squaw and a Red Flint strain.

For the dent inbreds there were 12 single crosses of inbreds from the same variety and 42 single crosses between inbreds originating from different varieties. Yields of the inbreds and of various types of crosses are given in Table 7.

Average yields of the five inbreds of Minn. #13 or the six inbreds of Rustler were considerably higher than the average of the four inbreds of Northwestern dent. Average yield of all 15 inbreds was 99 grams, that of all 42 single crosses between inbreds of different varieties was 311 grams and that of 12 single crosses of inbreds within a variety was 272 grams. If the average of single crosses within a variety is taken as 100, the comparative average yielding value of crosses between inbreds from different varieties is 114.3, while that of the inbreds themselves is 36.4 per cent.

Table 7 Average Yield of Dent Inbreds and F_1 Crosses in Grams per Hill

Variety or Cross	Type of Material	No. Inbreds or Crosses	No. Plots	Average Yield
Rustler	Inbred	6	12	108
Minn. #13	"	5	6	112
N. W. Dent	"	4	8	78
Within Rustler	F_1 cross	5	9	259
" Minn. #13	" "	3	6	303
" N. W. Dent	" "	4	8	266
Rustler x Minn. #13	" "	15	30	334
" x N. W. Dent	" "	17	33	300
Minn. #13 x N. W. Dent	" "	10	20	297

Table 8 Average Yield of Flint Inbreds and F_1 Crosses in Grams per Hill

Variety or Cross	Type of Material	No. Inbreds or Crosses	No. Plots	Average Yield
Longfellow	Inbred	4	8	115
King Philip	"	2	4	118
Squaw	"	2	4	61
Red Flint	"	1	2	84
Within Longfellow	F_1 Cross	4	7	261
" King Philip	" "	1	2	302
" Squaw	" "	1	1	258
Long. x K. P., Squaw and Red Flint	" "	14	28	309
King Philip x Squaw and Red Flint	" "	4	4	303

Similar results are given in Table 8 for studies with the flint inbreds.

Average yield of the four Flint inbreds from Longfellow and two from King Philip was greatly superior to that of the two Squaw and one Red Flint inbreds. Average yield of all nine inbreds was 100 grams, that of 18 single crosses between inbreds of different varieties was 308 grams and that of six crosses of inbreds within a variety was 268 grams. Taking 268 as 100 the average yield of crosses of inbreds from different varieties, and that of the inbreds themselves, becomes 115 and 37, respectively.

The inbreds used in these studies were selected from varieties in general adapted to the same environment. They were the ones that seemed most desirable on the basis of rather extensive selection in self-pollinated lines. More promising crosses eventually were produced using inbreds of more widely different origins. These first double crosses released by the Minnesota Agricultural Experiment Stations were Minhybrids 401 and 402 with the pedigrees, respectively, (11 x 14)(16 x 20) and (11 x 14)(15 x 19). The inbreds 11 and 14 were from Minn. #13 and inbreds 15, 16, 19, and 20 were from Rustler White.

The results of early trials of double crosses, including yield trials made from 1926 to 1930, inclusive, at various locations in Minnesota, were reported by Hayes *et al.* (1930) and by Hayes (1930). They appeared of sufficient promise so that Ralph Crim, Extension Agronomist, made 500 demonstrations of these two double crosses in 1930 and that year three one-acre seed plots were grown in cooperation with farmers for the production of double-cross seed. The first increases of these double crosses were described in the papers mentioned.

One of the difficulties of obtaining good double crosses from Minnesota corn varieties seemed to be that only a very small percentage of the selected inbreds had the ability to withstand lodging. Similar lack of standing ability was found in Nebraska by Kiesselbach with inbreds and crosses of Krug. It is of interest that the double crosses made by crossing Minn. #13 single cross (11 x 14) with (16 x 19) and (15 x 20) from Rustler, respectively, were outstanding in performance. It is fortunate that Jones used a double cross made by combining a single cross of Burr White inbreds with a single cross of Leaming inbreds for his first demonstration of the value of double crosses. Although the Burr-Leaming double cross from Connecticut was tested rather extensively in the Corn Belt it

was probably not widely adapted.

While Minhybrids 401 and 402 yielded rather well, they lacked popular appeal, as did the Burr-Leaming double cross, because of the segregation for kernel color on the ears of the cross. A few years later Minhybrid 301 was produced and released at Minnesota as a result of an interchange of inbreds with H. A. Wallace who furnished a late maturing inbred B164 to the writer in return for inbreds of Minnesota #13. The three-way cross, Minhybrid 301, (11 x 14)(B164), was introduced under a different designation by the Pioneer Company.

These results from Minnesota presented here are illustrations of the importance of genetic diversity. Other illustrations from Minnesota studies of the importance of genetic diversity, reviewed by Hayes, Immer, and Smith (1955), consisted of studies by Wu (1939), Hayes and Johnson (1939), and Johnson and Hayes (1940). Without doubt nearly every corn breeder has similar illustrations.

Andrés and Bascialli (1940) showed clearly the importance of genetic diversity. They compared the yielding ability of F_1 crosses between inbreds of North American and Argentine origins. The average yields of F_1 crosses between North American inbreds, Argentine inbreds, and crosses of North American x Argentine inbreds, are summarized (See Table 9).

The 15 crosses between North American inbreds gave an average yield of 3871 kilograms per hectare and exceeded the average of 48 crosses between Argentine inbreds by 7 per cent. However, the 34 crosses of North American with Argentine inbreds exceeded the average of crosses between North American inbreds by over 11 per cent. The highest yielding single cross was a combination of a North American inbred with an Argentine inbred.

Eckhardt and Bryan (1940b) at Iowa presented data from a series of double crosses that likewise emphasized the value of genetic diversity. They selected inbreds from different varieties by the usual methods. Designating inbreds from one variety as A and B and those from another by X and Y, they compared the relative value of the double crosses (A x B)(X xY) with those of (A x X)(B xY) and (A x Y)(B x X). The double crosses (A x B) (X x Y) proved distinctly superior, on the average, to the other combinations.

A more recent research (Griffing and Lindstrom, 1954) consisted of a study of combining ability of inbreds from various breeding sources.

Table 9 F_1 Hybrids among Inbreds of Different Origins

Origin	No. Crosses	Kilograms per Hectare	
		Highest Cross	Average
North American	15	5155	3871
Argentine	48	5566	3618
N. A. x Argentine	34	5694	4317

For an analysis of their results from the viewpoint of genetic diversity the inbred line material may be placed in three groups.

A. Cycled inbreds, the 3 better appearing inbreds from crosses, and subsequent selection in selfed lines with Corn Belt inbreds as parents.

B. Brazilian inbreds, the 3 better appearing inbreds selected from material partially inbred and introduced by Lindstrom from Brazil, that was further inbred and selected at Ames for desirable appearing characters. The writers thought it probable that the "bulk of the germ plasm traces back to Southern United States dents imported into Brazil, acclimatized to Brazilian conditions, and contaminated to various degrees by native corn types."

C. Exotic inbreds, the 3 better appearing inbreds selected from crosses and back crosses of Corn Belt lines with Mexican inbreds. Each of 3 Mexican inbreds was crossed with Corn Belt inbreds, and in some cases the F_1 cross was subsequently crossed to a different Corn Belt inbred. Subsequent selection in selfed lines was practiced. In the Exotic group two lines E_8 and E_9 were somewhat similar in their Corn Belt parentage.

No previous studies of the combining ability of the 9 selected inbred lines had been made. All possible diallel crosses were studied as well as the 9 inbred parents. Single hill studies were made so that the characters of individual plants could be determined.

A brief summary of yield and tasseling date of the 3 groups of inbreds is given in Table 10.

The average yield of the 3 Exotic lines was 151 grams per hill, that of the Cycled lines 139 grams, and that of the Brazilian lines 126 grams. The 3 Cycled inbreds tasseled considerably

Table 10 Range of Yields in Grams per Hill, Average Yield, Range in Tasseling Date and Average Tasseling Date in Days, of 3 Groups of Inbred Lines

Inbred Group	Range of Yield	Average Yield	Range, Tasseling Date	Average Tasseling Date
	grams	grams	days	days
Cycled	116 - 169	139	13 - 14	13
Brazilian	99 - 147	126	19 - 21	20
Exotic	88 - 203	151	15 - 22	18

earlier than the 3 Brazilian or 3 Exotic lines. That these 9 lines are somewhat superior to the lines first selected from varieties seems evident if one compares the average yield of the inbreds with the average yield of their F_1 crosses within each group. This would consist of a comparison of the average of 3 inbreds with 3 crosses for each group. For the Cycled group the average yield per hill of 3 inbreds was 139, that of Cycled crosses 236; the average yield of the 3 Brazilian inbreds was 126, that of Brazilian crosses 218; while with the 3 Exotic inbreds the average yield of inbreds was 151 and that of F_1 crosses was 278. If the average yield of single crosses in each of the 3 groups is taken as 100, that of the inbred parents in the Cycled group was 59, the Brazilian group 59, and the Exotic group 54 per cent. It seems evident that these 9 inbred lines perform better as inbreds than a large part of the inbreds used in hybrid corn production.

Considering the F_1 crosses there are 3 possible single crosses within each group, and 3 possible single crosses of each inbred with inbreds belonging to each of the different groups. As there are 3 inbreds within a group, there are 9 possible single crosses of inbreds of one group with inbreds of another group. Results are given in Table 11 from crosses within and between groups.

Average yield of crosses within the Brazilian group was 218 grams, that of crosses of Brazilian x Cycled 233 grams and that of Brazilian x Exotic 258 grams. Crosses between groups average 6.4 and 18.8 per cent more than crosses within groups.

Table 11 Average Yields in Grams and Dates of Tasseling in Days and Types of F_1 Crosses

F_1 Crosses	No. Crosses	Yield per Hill (grams)		Days Tasseling (days)	
		Range	Average	Range	Average
Cycled x Cycled	3	209 - 260	236	28 - 35	32
Brazilian x Brazilian	3	214 - 234	218	36 - 43	40
Exotic x Exotic	3	273 - 302	278	35 - 41	38
Cycled x Brazilian	9	184 - 258	233	31 - 45	36
Cycled x Exotic	9	214 - 300	250	29 - 40	33
Brazilian x Exotic	9	197 - 284	258	33 - 44	40

It seems probable that the Brazilian inbreds, even though rather highly selected, are not sufficiently desirable in overall characters so that they could be used directly in single or double crosses for commercial production.

Cycled x Cycled crosses gave an average yield of 236 grams, while Cycled x Exotic gave an average yield of 250 grams, or nearly 6 per cent over Cycled x Cycled. Both inbred parents in these crosses would seem relatively well adapted agronomically to the Corn Belt.

Exotic x Exotic crosses gave an average yield of 278 grams, which is greater than that of any other group; approximately 10 per cent higher in yield than Cycled x Exotic and 7 per cent higher than Brazilian x Exotic. The two highest yielding single crosses were a cross of Exotic x Exotic, at 302 grams, and a cross of Cycled x Exotic, 300 grams. However, all 3 crosses of Exotic x Exotic yielded more than any single cross of Cycled x Cycled or Brazilian x Brazilian.

These results indicate rather clearly that genetic diversity in the inbreds to be used in double crosses is desirable. Griffing and Lindstrom conclude that heterosis is related to some extent to genetic diversity and that the breeder located in the Corn Belt should maintain Corn Belt standards.

Unpublished results of breeding studies carried out by Dr. Y. S. Tsiang and his associates in Taiwan have been included with their permission. Dr. Tsiang completed his graduate work at Minnesota about twenty years ago and for several years while here he was in direct charge of corn breeding at the

Waseca Station of the Institute of Agriculture, Department of Agronomy and Plant Genetics. On returning to Taiwan, where he now is one of the five Commissioners of the Joint Commission of Rural Reconstruction, he has carried on corn breeding during Saturdays and Sundays when time was available.

In these studies Dr. Tsiang and his associates have utilized American inbreds in their program. Selected inbreds have been produced also from Taiwan tropical flint varieties. They now have a double-cross hybrid of the following pedigree, (single cross of Ohio inbreds)(single cross of tropical flints), that in twenty-six replicated trials at various localities has yielded an average of 104 bushels, 78 per cent more than the standard open pollinated flint, and that matures three to four weeks earlier than the tropical flint variety now grown. In breeding the flint inbreds he used the well-known method of selection in self-pollinated lines. His final cross makes use of genetic diversity in a very basic and practical way.

The importance of genetic diversity has been stressed in this review as it is a basic principle of great value to the breeders of hybrid corn.

Chapter 8

GENERAL AND SPECIFIC COMBINING ABILITY

Introduction

Selection in self-pollinated lines is the first step followed by corn breeders in the production of inbreds for eventual use in crosses. The usual method is to select visually, under conditions of self-pollination, for the plants and lines having the more desirable combination of characters. The particular objectives are vigorous inbred lines, free from abnormalities, that excel in vigor characteristics, that have good pollen and ear development, desirable seed characters, ability to withstand lodging (usually correlated with root development), and that have as great resistances as possible to diseases and insect pests.

Special methods have been developed to determine standing ability, such as resistance to pulling and size of root clump when pulled from the ground by artificial means as the plants approach maturity. Also special technics have been developed to study, under controlled environmental conditions in some cases, resistance to diseases and insect pests, ability to germinate under low temperatures, and other desirable characteristics.

After the more desirable appearing inbreds have been isolated they are studied for general combining ability. Those inbreds that survive this test are then used in studies to determine specific combining ability and making single, 3-way or double crosses.

General combining ability may be defined as the comparative ability of a group of inbreds to combine with a tester or group of testers. Inbred-variety crosses have been used rather generally, as a variety furnishes a diverse type of germ plasm

when used as a tester. Desirable single and double crosses also have been used as testers, although, as will be discussed later, there may be reasons why the most desirable single or double cross, for the general region of adaptation, may not be a satisfactory tester.

Specific combining ability in many cases may be defined as the deviation in performance of a specific single cross from the performance expected on the basis of general combining ability.

If, however, in a particular breeding program the breeder tests a series of inbreds in crosses with a particular inbred or single cross, in order to obtain the best inbreds for use in this combination, it seems to the writer that this should also be called a study of specific combining ability. In this case the general combining ability of the lines tested is unknown.

Sprague and Tatum (1942) recognizing the importance of both general and specific combining ability, and their differentiation, presented a method of comparing general and specific combining ability of a group of inbreds. They suggested using approximately 10 inbreds in each such study and making all possible diallel single crosses between these inbreds.

They determined general combining ability of each inbred by averaging the results from all single crosses of each inbred. These averages were used to compare the general combining ability of the inbreds in the study. To determine the relative importance of general and specific combining ability in each study of diallel crosses, statistical constants were calculated. General combining ability expressed as a statistic shows the extent of deviation of the mean yield of the single crosses involving each inbred from the averages of all single crosses. The statistical constant for specific combining ability expresses the extent of deviation of individual crosses in which this inbred is one parent from the mean of all single crosses of that inbred with other inbreds.

The method seems of greatest interest as a means of comparing the relative magnitude of general and specific combining ability in a group of inbreds. Where these inbreds represent a random sample from a population, the values obtained from general and specific combining ability are assumed to be estimates of these values for the whole population. If the inbreds have been selected for high general combining ability prior to use in the diallel cross, a common procedure in actual breeding programs, the statistic obtained for general combining ability

will tend to be low relative to that for specific combining ability even though all of the lines have high general combining ability.

The plant breeder is interested primarily in single crosses which excel in comparison with other single crosses. For this reason, and because of the importance of general combining ability of the inbreds in determining single cross performance, the plant breeder usually selects first for general combining ability. Then among the lines having high general combining ability, he is interested in those combinations which have the highest single cross performance. Because the effects of genetic diversity on combining ability, two lines with high general combining ability but similar genetic make-up would produce a single cross with low performance relative to that expected. This would result in a high statistical value for specific combining value for each of these lines even though the resultant cross was not needed in the breeding program.

In many cases check varieties or hybrids of known performance are used as a standard, or standards, in yield trials made to test either general or specific combining ability or for both types of combining ability.

Studies of General Combining Ability

Davis (1929) made the first suggestion for the use of inbred-varietal crosses as a means of testing for general combining ability. Jenkins and Brunson (1932) presented extensive evidence that showed inbred-varietal crosses were as reliable a method of testing for general combining ability as the average of separate tests with a group of 9 to 12 unrelated inbreds. These studies have been reviewed more completely in chapter 6.

Johnson and Hayes (1940) and Cowan (1943) classified inbreds for general combining ability based upon inbred-varietal performance. As the number of inbreds used in each of the studies was small, they were divided, based on the test cross results, into two groups called low and high combiners. Certainly in the center of the range the low combiners were not significantly lower than the high combiners that were close to the division point between the two groups. However, it was considered desirable to include all of the material in the study instead of selecting the extremes.

The inbreds studied by Johnson and Hayes had been selected from different origins to eliminate as far as possible those

combinations that would bring together inbreds that were of similar parentage. Single crosses were made between inbreds belonging to the two groups for general combining ability, including high x high, high x low, and low x low. The single crosses were classified into yield performance groups. The average performance of the checks was considered as class 0, and other classes included +1 to +2, -1 to -2, etc., of the calculated standard error of a difference. The results are given in Table 12.

Low x low crosses, on an average, were distinctly lower in mean yield than high x high or high x low. High x high and high x low crosses yielded about the same, on the average. There was a tendency for high x low to show a somewhat wider range of variability in both directions than high x high, although it was not possible to determine whether this was a significant difference.

Cowan's study was carried out in a manner similar to that of Johnson and Hayes. He used only twelve inbred lines, and these were placed in two groups. The A group included one inbred of Minnesota #13, three from Lancaster, and one from an origin called 22-118, while the B group included seven inbreds each of which originated from a different plant of the Bailey variety.

These inbreds were classified for general combining ability on the basis of yields of top-crosses with Harrow Golden Glow, a variety not related closely to any of the inbreds. The top-cross yield trial consisted of eight replications and on the basis of these results the lines were classified as having low or high general combining ability. Top-crosses considered as examples of low combiners ranged in yield from 70 to 82 bushels, while those classified as high combiners ranged in yield from 83 to 107 bushels.

An attempt to make all possible combinations between inbreds gave the results presented in Table 13.

Yield comparisons of the single crosses were made in a lattice design with eight blocks of eight plots each and four replications. The calculated standard error was 5.8 bushels. Using Golden Glow as a standard, and considering its yield to be class 0, the single crosses were placed in classes in a frequency distribution ranging from -7 to +7 times the standard error of a difference from Golden Glow.

The low x low crosses averaged significantly lower in yield than the low x high or high x high crosses, while the low

Table **12** Summary of Frequency Distribution of Single-Cross Yields at Three Locations with Three Replications at Each Location, When Compared with Recommended Double Crosses of Similar Maturity in Relation to the General Combining Ability of Their Inbred Parents

Type of Cross	Class centers of + and - 1 to 8 times the standard error of a difference									Total Crosses	Mean class value
	-7 to -8	-5 to -6	-3 to -4	-1 to -2	0	+1 to +2	+3 to +4	+5 to +6	+7 to +8		
Low x low	..	1	1	2	4	4	..	..	..	12	-0.50 ± .66
Low x high	1	3	..	11	6	16	9	5	1	52	+1.06 ± .42
High x high	..	1	5	12	8	33	20	4	..	83	+1.10 ± .24

Table **13** Frequency Distribution of Single-Cross Yields When Compared with Harrow Golden Glow as a Check in Single-Crosses of the Three Types, High x High, High x Low, and Low x Low

Type of Cross	Class centers of ±1 to 7 times the standard error of a difference								Total Crosses	Mean
	-7	-5 to -6	-3 to -4	-1 to -2	0	+1 to +2	+3 to +4	+5 to +6	+7		
Low x low			5	5		1				11	-2.3 ± .43
Low x high	1	1	4	4	7	5	9	0	1	32	+0.5 ± .54
High x high			1	3	1	2	1			8	-0.1 ± .79

x high and high x high were about equal in average yielding ability. As there were only eight crosses in the high x high group and thirty-two in the high x low, it is difficult to compare ranges of yield between the two groups.

Jenkins (1935) studied the general combining ability in test crosses of eight inbreds that had been selfed from one to eight generations. From a study of yields in test crosses he concluded that the general combining ability became fixed early in the breeding process and that further inbreeding had little influence on combining ability. At the suggestion of the writer, the late Dr. F. R. Immer reanalyzed Jenkins' data but was unable to substantiate Jenkins' thesis. Later Richey (1945b, 1947) reanalyzed Jenkins' data. Richey concluded, as Immer had previously, although Immer's study was not published, that the inbreds changed markedly in relative combining ability during the process of selection in self-pollinated lines through the eight generations of inbreeding. That such changes do occur during selection in self-pollinated lines was the conclusion also from the study by Payne and Hayes (1949).

Early testing was proposed by Jenkins as a result of the 1935 study. As used today it is based on two assumptions. First, that there are marked differences in the combining ability among open-pollinated S_0 plants, and second, the sample selected through the testing of S_0 or S_1 plants should yield more desirable material for further inbreeding than plants selected by visual means alone. The technic of early testing will be given in greater detail later. It consists of selecting individual plants in early generation populations, selfing each and using pollen of each of these selected plants to cross with a tester. Inbreeding then may be continued only with lines that are high combiners as determined by test crosses. This study was reviewed here as early testing was one of the technics used in studies of general combining ability by Green.

Green (1948) made an interesting study of combining ability. In a comparison of all possible single crosses between thirteen selected inbreds, some of which have been used extensively in double crosses, the general combining ability of each was determined from all possible twelve crosses. The mean yield of all seventy-eight crosses was 85.7 bushels. The average yields of single crosses involving four selected inbreds were as follows:

Inbred	Average Yield of 12 Crosses
	Bushels
I 198	91.8
M 14	90.2
KB 397	83.5
Ill. 4226	80.5

I 198 and M 14 were considered to have high general combining ability, and KB 397 and Ill. 4226 low general combining ability. Three types of crosses among these four inbreds were used in the study, namely, I 198 x M 14 (high x high), I 198 x KB 397 (high x low), and KB 397 x Ill. 4226 (low x low).

Approximately 150 plants within the F_2 population of each of the three crosses were selfed and top-crossed onto two testers, using for this purpose five plants of the standard double cross, U.S. 13, and ten plants of the open-pollinated variety, Black's Yellow Dent.

The 83 F_2 plants which were more desirable agronomically were selected from each of the three crosses and the top-cross combining ability determined from an average of the two tester crosses. The 83 top-crosses with each of the two testers of 83 plants from each F_2 population and the three parental single crosses were included in yield trials made in 1945 and 1946, using an 8 x 8 x 8 cubic lattice design.

The average yields are summarized in Table 14.

It is of interest that the three original single crosses in this case differed widely in yielding ability. The low x low, or KB 397 x Ill. 4226 yielded only 58.4 bushels, while the other two, (low x high) and (high x high), yielded 72.4 and 80.0 bushels, respectively. In the crosses of the parental single crosses with the two testers, referred to in the table as testers x parental singles, however, the three had about equal average combining ability. As the three goups of 83 selected plants when crossed with the two testers differed significantly in combining ability, on an average, the two types of results seem rather difficult to explain. Even though they differed significantly, the differences among the three averages of the top-crosses were not very great. The test crosses of F_2 plants from low x low gave an average yield of 68.8 and those from high x high had an average yield of only 73.6 bushels.

To the writer these results seem best explained by the following hypothesis. U.S. 13, a desirable double-cross hybrid was used as one top-cross parent, and the results were averaged with the top-crosses with Black's Yellow Dent. Previous studies

Table 14 Average Yields of the Top-Crosses with U.S. #13 and Black's Yellow Dent and of the Parental Single Crosses

Original Cross	Top-Crosses of F_2 Plants	Testers x Parental Singles	Original Single Crosses
	Bu.	Bu.	Bu.
High x high	73.6	70.5	80.0
Low x high	72.0	70.6	72.4
Low x low	68.8	69.4	58.4

reviewed show that high x low yields about as well as high x high. Green found that F_2 plants of high x high did not differ significantly, on the average of 83 top-crosses, from F_2 plants of high x low; however, the test crosses of F_2 plants of low x low were definitely lower in average yield than the other two types. It seems probable that U.S. #13 double cross produced mostly gametes of high combining ability, and this may have reduced the variability of average yields in test crosses of F_2 plants of the three hybrid populations. When all of the 83 F_2 plants were of the low x low combination, this led to a lower yield of their top-crosses. Subsequently Sprague (1959) has emphasized the fact that Black's Yellow Dent used as a tester differentiated the combining ability better than U.S. #13 although he gave no definite explanation as to the cause.

Studies of Specific Combining Ability

Unpublished[1] research studies of the writer and his colleagues at the Minnesota Agricultural Experiment Station were used in the study of specific combining ability. This material consisted of 15 inbred lines used in breeding studies for the production of double-crosses for South Central and Southern Minnesota. These 15 inbreds are unrelated to each other, so far as is known, and therefore have the desirable characteristic

[1]The original data were taken under the immediate direction of Drs. E. H. Rinke, E. L. Pinnell and others. Dr. Rinke very kindly made the data available to the writer and also furnished a research assistant to aid in the calculations. The writer acknowledges his indebtedness to his colleagues and his appreciation of their courtesy in making the data available. The writer is responsible primarily for the analysis of the data as presented.

of genetic diversity. They are a group of elite inbred lines, many of which have been proven to have desirable combining ability in crosses. Five of the inbreds, A73, A395, A334, A302, and A375, are Minnesota lines. Of these, A73 was obtained from Wisconsin but had not been used in released crosses. To what extent this inbred was modified by selection under Minnesota conditions is unknown; therefore it was given a Minnesota designation. A375 is a selection of Holbert's A that matures somewhat earlier than the original A inbred from Holbert, A334 was selected from Golden King, while A395 and A302 were obtained by selection from crosses of inbreds. Wf 9 and Fe, from Indiana, have been used widely in double-crosses throughout the Corn Belt; Oh51A and Oh40B are well known inbreds from Ohio; IaY82 and Ia234 are promising inbreds from the Iowa Station, CC25 and CC27 are from Wisconsin, while Ill. 4226 was obtained from the Illinois Station.

These inbreds have been grown in yield trials at the Waseca Station in comparison with Minhybrid 403 and the standard inbred A374. When grown during different years the results were adjusted in relation to the performance of the standard inbred A374. It deserves emphasis that the years in which these tests were conducted were relatively desirable seasons for corn, and the extent of variability from season to season was not very great in these trials.

The results of the inbred trials are given in Table 15. While other data were taken, those presented seem adequate for illustrative purposes. These include averages for height of plant, ear length, good ears per plant, percent moisture of the grain at husking, and yield in bushels per acre. Each of the inbreds was crossed with all others, and the average results for yield and moisture are presented in Table 15 as a performance index in relation to double cross Minhybrid 403, since it is well adapted and usually matures satisfactorily. A performance index is used as under Minnesota conditions there is a rather direct positive relation between total yield on a 15.5 per cent moisture basis and time of maturity, later hybrids yielding more, on the average. The performance index used here consists of placing moisture percentage and yield in terms of Minhybrid 403 as 100, a procedure developed through many years of experience.

For the single crosses positive increases in moisture percentage over Minhybrid 403 as 100 are given a negative value and lower percentages of moisture in relation to Minhybrid 403

Table 15 Performance of Inbred Lines in Yield Trials and Average Performance of Their F_1 Crosses

Inbred	Years Tested	Height Plant In.	Ear Length In.	Good Ears per Plant	% Moisture	Yield Bu.	Performance Index In Relation to Minn. 403 Inbreds	Av. of Crosses
Wf9	1943	74	5.9	.80	43.6	25.0	27	106
Os420	1941-43	78	6.6	.80	38.2	36.7	49	98
Oh40B	"	69	7.5	.71	27.8	27.6	44	93
CC25	"	72	6.3	.93	35.7	31.1	42	110
CC27	"	78	6.2	.59	38.9	36.5	48	105
IaY82	1942-43	78	7.1	.87	21.4	37.0	64	113
FE	1941-43	64	5.7	.65	36.3	29.0	39	103
Ia234	1941-42	93	5.9	.81	36.3	30.7	41	110
Oh51A	1941-43	67	5.9	.91	28.8	32.7	51	113
A73	1940-43	63	6.4	.85	34.4	32.6	46	111
A395	1943	92	6.5	.80	39.4	35.2	46	110
A334	1939-43	61	4.5	.75	28.0	17.2	27	105
A302	1943	70	5.9	.79	31.6	25.3	37	105
A375	1939, 1941-43	75	5.7	.87	27.1	28.2	45	106
Ill.4226	1941-42	73	5.9	.95	33.4	32.9	47	105
Average		74	6.1	.81	33.4	30.5	44	
Minn403	1941-42	92	7.8	.97	25.6	67.0	100	
A374	"	69	6.4	.87	26.5	29.7	45	

are given a positive value. For yield, in percentage of Minhybrid 403 as 100, the increased percentage over 100 is given a positive value, and a lower percentage a negative value. Adding these values for percentages of moisture and yield for each inbred or single cross with attention to their signs, gives a value which when added to or subtracted from 100 is used as the performance index.

To develop a performance index for the inbreds they were first compared with A374, a desirable inbred from the standpoint of performance as an inbred. In this case also a moisture percentage value over 100 is given a negative sign, but for inbreds this value is divided by two, as inbreds usually produce crosses that are lower in moisture at husking than their inbred parents. Yield percentages in relation to A374 as 100 are given full value. After adjusting to A374, the inbreds were then adjusted in relation to Minhybrid 403. In this case also a positive percentage increase in moisture at husking of the inbred over Minhybrid 403 was reduced to half its actual value by dividing by two.

One inbred, IaY82, had a performance index of 64, and several inbreds had performance indices around 50 per cent of the double-cross check. These inbreds are a great deal more desirable than the inbreds available during the early years of hybrid corn breeding.

It is of interest to note the relation of characters of inbreds to the average for the same character in the 14 possible crosses involving each inbred. The correlation coefficients are given in Table 16.

Table **16** Correlation Coefficients for Various Characters of Inbreds and the Average of All Possible 14 Crosses

Character	Correlation Coefficient
Height of plant	.64
Ear length	.74
Good ears per plant	.73
% Moisture at husking	.35
Yield in bushels per acre	.13
Performance index	.22

r values for degrees of freedom of 13, for P of .05 = .51 and for p of .01 = .64

Correlations for height of plant, ear length, and good ears per plant were highly significant. The other r values for maturity and yield, while positive, were below the 5 per cent point. A part of the difficulty in this case may be due to the rather low yield of inbred Wf 9 and its correspondingly high moisture percentage at husking. This inbred is too late in maturity to be handled easily at the Waseca Station.

Yields in bushels per acre of all possible single crosses between the fifteen inbreds, and the inbreds themselves are given in Table 17. The yields of the inbreds themselves ranged from 17.2 bushels to 37.0 bushels; while the average yields of 14 single crosses of each inbred ranged from 75.1 bushels to 84.6 bushels. It is apparent that high yielding double crosses can be obtained from several different combinations of inbreds.

Another point deserves special comment. Minhybrid 403

Table 17 Yield in Bushels per Acre of Inbreds and F_1 Crosses

	Wf9	Os420	Oh40B	CC25	A73	CC27	IaY82	A395	FE	Ia234	Oh51A	A334	A302	A375	Ill.4226	Average
Wf9	25.0	88	81	85	84	85	81	93	88	86	79	86	79	86	84	84.6
Os420		36.7	90	90	91	94	61	83	73	81	81	81	88	84	79	83.1
Oh40B			27.6	86	84	75	79	85	83	78	72	76	78	81	76	80.3
CC25				31.1	81	78	83	88	77	80	82	79	74	74	72	80.6
A73					32.6	75	89	79	79	82	84	78	77	73	68	80.2
CC27						36.5	79	73	79	85	84	76	72	70	74	78.7
IaY82							37.0	83	77	84	80	79	85	72	74	79.3
A395								35.4	81	86	74	74	80	75	69	80.3
FE									29.0	70	81	76	76	83	72	78.3
Ia234										30.7	79	66	83	72	77	79.2
Oh51A											32.7	80	77	75	71	78.6
A334												17.2	73	73	79	77.0
A302													25.4	73	79	78.3
A375														28.2	74	76.2
Ill. 4226															33.9	75.1

was a good hybrid for many years and was grown extensively and was well liked by corn growers. The average of all single crosses of each of six of the fifteen inbreds excelled Minhybrid 403 by 10 per cent or more.

Table 17 shows the type of yield results obtained when unrelated inbreds are studied in all possible F_1 crosses. Only a small phase will be summarized with particular reference to specific combining ability. For this purpose only data with respect to performance index will be reviewed.

Since each inbred was crossed with 14 other inbreds the general combining ability of each inbred can be determined from averaging all crosses of that inbred with other inbreds. On the basis of this estimate of general combining ability the fifteen inbreds were placed in three classes for performance index as follows:

L, inbreds ranging for general combining ability from 93-103, consisting of inbreds Os420, Oh40B, and Fe

M, inbreds ranging from 105-106 including Wf9, CC27, A334, A302, A375, and Ill. 4226

H, inbreds ranging from 110 to 113 including CC25, IaY82, Ia234, Oh51A, A73, and A395

Results with this type of classification for all possible F_1 crosses are given in Table 18.

There were wide deviations in performance index for all three types of crosses L x L, L x M, M x H etc. The highest class for performance index was 130 containing 3 single crosses of H x H classification for general combining ability and one single cross of M x H. The lowest class for performance, or 74, contained one cross each of L x L and L x H. The H x H group consisting of 15 single crosses had a mean value of 118 and a range for classes from 109 to 130, while L x L with only 3 crosses ranged from 74 to 109, with a mean of 88. These results give evidence that testing inbreds for general combining ability seems worth while in relation to the specific performance of individual single crosses.

These results are evidence supporting the conclusion that single crosses of extremely high performance, in comparison with averages of all single crosses, could not be expected to occur very frequently unless one of the inbred parents excelled in general combining ability. This seems to this reviewer to be logical. The results also seem to emphasize the importance of selecting inbreds that excel in agronomic characters, and in general combining ability, and to maintain as far as possible

Table 18 Relation Between Performance Index Classes for General Combining Ability and Yield of F_1 Crosses

Yield Classes for General Combining Ability	Classes for Performance of F_1 Crosses									No.	Mean
	74	81	88	95	102	109	116	123	130		
L x L 93 - 103	1	1				1				3	88.0 ± 10.7
L x M		1	5	3	5	1	2	1		18	98.9 ± 2.7
L x H	1	3	1		6	2	5			18	100.8 ± 3.3
M x M 105 - 106		1		3	4	3	3	1		15	104.8 ± 2.8
M x H			1	1	9	10	10	4	1	36	110.4 ± 1.5
H x H 110 - 113						3	8	1	3	15	117.9 ± 1.9

rather wide genetic diversity.

Another fact seems of considerable interest. There were four single crosses out of 105 that excelled Minhybrid 403 by about 30 per cent. These results also lead to the conclusion that there still remained an excellent opportunity of developing improved crosses that greatly excel those previously grown that were obtained from first cycle breeding.

As another illustration of studies of specific combining ability and their importance, one of the projects now being carried out cooperatively by corn breeders in the North Central Region will be outlined briefly. Three-way crosses are being made to find improved inbreds that combine well with such single crosses as (Wf9 x M14) for the northern area and with some combinations of Wf9 with other inbreds for other areas. These breeding programs illustrate how studies of specific combining ability can be carried out in a definite, planned program.

Wf9 from Indiana has been used more extensively in double crosses than most other inbreds. As a rule it gives excellent seed quality to its hybrids and therefore it often is used as one the inbreds in the female parent of double crosses. While somewhat later in maturity than is desirable for Southern Minnesota, with higher moisture content at husking than any of the fifteen inbreds used in the diallel crosses previously discussed, seed growers even in Southern Minnesota appreciate the value of Wf9.

Wf9 appears to have average general combining ability for yield; in this respect it is not equal to some very outstanding inbreds. Wf9 also excels in some plant characters. On a performance index basis, as explained previously, its calculated value in comparison with 14 other inbreds in Minnesota studies

was 106, where the mean performance index was 106.2. Two inbreds gave a mean performance index of 113 based on the average of their 14 crosses and four other inbreds exceeded the value of 106 by 4 or more. Only two inbreds were distinctly lower than Wf9 in average general combining ability. Its wide use in hybrids, therefore, seems to be the result primarily of favorable genes for seed quality.

While Wf9 has many desirable characters that have led to its wide use as one of the inbreds of the seed parent, it is very susceptible to early and late attack of the corn borer. Wf9 when infested with many corn borer larvae, perhaps because of stalk characteristics, often appears to be more tolerant than many inbreds to borer attack and it seems to transmit this tolerance to its hybrid progeny. Cooperative studies to breed inbreds equal to Wf9 as a seed parent and to improve its other characters where possible would seem equally or more valuable than the acceptance of Wf9, with the idea of obtaining inbreds that combined well with it in its present form.

Testers for General and Specific Combining Ability

In a recent discussion of Green's studies, Sprague (1959) states that there were highly significant differences between the three groups, high x high, high x low, and low x low, when Black's Yellow Dent alone was used as the tester. Sprague in this review refers to Davis (1934) and others as suggesting the desirability of a low yielding variety, susceptible to lodging, that might approximate the multiple recessive type as a tester for general combining ability. He presents some reasons for his present viewpoint that this usually may not be the most desirable tester.

Sprague emphasized that the tester should differ in origin from the lines to be tested and should be heterogeneous as such material would be more widely adapted to different locations and environments. The general recommendations as given, altho not so stated by Sprague, seem to be more directly related to tests for specific combining ability than for the purpose of selecting lines that have high general combining ability.

Federer and Sprague (1947) carried out studies to compare the relative efficiency, with a fixed number of plots, of increasing the number of replicates or the number of testers. Increasing the number of testers to determine general combining ability

was more valuable.

Sprague states that in tests for general combining ability in the early phases of a breeding program, open-pollinated varieties would be the only testers available. His final conclusion is that most of his recommendations for testers, based on Iowa studies, can be achieved by using as a tester a synthetic variety made up of the most widely used inbred lines within a maturity zone. If Green's results and those of Johnson and Hayes, and Cowan, previously discussed, are kept in mind, it was found to be difficult to obtain an adequate test for general combining ability by using a tester that in itself had high yielding ability.

This leads the writer to conclude that in tests for general combining ability, for the first isolation of inbreds to use in further studies of specific combining ability, the tester should be genetically diverse from the lines to be tested, adapted to the region where the inbreds are to be used in crosses, and should consist of material that previously has not been selected for high combining ability. In the early stages of a breeding program, as Sprague suggests, a desirable adapted variety may be the most useful tester for general combining ability. It seems probable, however, that a synthetic produced from low combining lines, that are recessive, or partially so, for important growth factors, would be desirable to use in testing for general combining ability. This suggestion, or its equivalent, has been made previously by both Sprague and Tatum and Davis.

In tests for specific combining ability the tester, where feasible, should consist of material with which the improved inbreds will be used in hybrid combination. In this case it may be desirable, in some cases, to use a Synthetic composed of inbreds now widely used in the region where the new hybrids will be grown. In many cases, and it seems to the writer that in most cases, the test for specific combining ability will be made directly with the inbreds, or crosses, with which the selected inbreds will be used.

Sprague (1939) presented data which led him to conclude that the mixture of pollen from 10 plants taken at random would represent satisfactorily the germ plasm of an open-pollinated variety.

Chapter 9 HETEROSIS

Introduction

Before preparing this phase of the summary in relation to hybrid corn history the writer again has consulted pertinent papers from recent summaries, including those in "Heterosis." This book (Gowen 1952) consists of thirty papers presented, and extensively discussed in subsequent seminar periods held from June 15 to July 20, 1950, by research workers who were in attendance at the heterosis conference at Ames, Iowa. Another interesting and more recent publication consists of thirteen papers in the Proceedings of the Royal Society, Vol. 144. This conference was under the leadership of Mather (1955a) with a general title, "A Discussion of Hybrid Vigor."

A statement from the preface in "Heterosis" was as follows, "The return from hybrid corn has been phenomenal, but it is now evidently approaching an asymptotic value." It is evident that if one compares the end results of the first utilization of heterosis with the yield of open-pollinated corn, this represents the effects of the first cycle of breeding. For the second cycle, however, the comparison is made with the performance of the first cycle as a standard and it seems reasonable to expect that it may be more difficult to obtain as great an increase in performance, in most cases, as when hybrids were compared with open-pollinated varieties.

Hull (1952) writes, "Initial successes with hybrid corn

The writer expresses his appreciation for valuable suggestions from Dr. C. R. Burnham regarding the chapters on Heterosis and Genetics and Cytogenetics of Corn.

(which so far have not been greatly surpassed) were obtained with inbred lines which were, for the most part, isolated directly from open-pollinated varieties," and in a further discussion of his results with second cycle hybrids he writes, "My first suspicion that all was not well was aroused by disappointing yield performance of second cycle hybrids in 1941." This led Dr. Hull to devise a plan of recurrent selection for specific combining ability with an inbred as the tester. It is evident also that Hull suggested recurrent selection because he thought this method more satisfactory if heterosis was dependent in a large part on over dominance.

Comparison of First and Second Cycle Breeding

Discussions of the results of second and subsequent cycles of breeding will be presented in later chapters in relation to various methods of breeding. Improvements in performance from second and later cycles have been obtained not only for yielding ability but also for resistances to diseases, insect pests and for other characters that are of great value to the corn grower. These experiments lead the writer to conclude that second and subsequent cycle breeding often has proven of great value, even though some of the results of second cycle breeding have not been as outstanding as nearly all of the first cycle results may seem to be. A brief review of some Minnesota studies will be made.

It has been emphasized previously that from the first cycle of breeding in Minnesota no double cross of great promise was obtained when inbreds from a single variety were combined in a double cross. From using inbreds of Minnesota #13 for one of the single-cross parents in (11 x 14), and inbreds from Rustler for the other single-cross parents, (15 x 19) and (16 x 20), Minhybrids of mixed seed color, called Minhybrids 401 and 402, were produced. These were the first hybrids that were used to demonstrate hybrid vigor in Minnesota in the early years of Minnesota studies, and these two double crosses were grown rather extensively in the nineteen thirties by Minnesota farmers and also in North Dakota. One objection to these double crosses was their mixed seed color. Although they lacked as desirable standing ability as double crosses produced later they were superior to open-pollinated Minnesota varieties not only in yielding ability but also in standing ability.

The next step forward resulted from crossing the single cross of Minnesota #13 inbreds, (11 x 14) with a later maturing inbred B164 obtained from Wallace that had the capability of producing sufficient pollen and had also good combining ability as a male parent. A three-way, (11 x 14)B164, named Minhybrid 301, was introduced and grown rather extensively. Further selection within inbreds received from Holbert in 1928 resulted in the isolation of two inbreds that were of somewhat earlier maturity than the original Holbert A line. Two closely related inbreds selected from this A line were called A374 and A375. The cross of these two lines gave sufficient vigor to use as a male parent for the double cross Minhybrid 403, (11 x 14)(A374 x A375). It seems probable that both Minhybrids 301 and 403 should be considered as the result of first cycle breeding; however, they had the advantage of wide genetic diversity between the male and female parents of the double cross.

Second cycle breeding in Minnesota was started in 1928 (Hayes and Johnson, 1939) by crossing several inbreds introduced from other breeders in the Corn Belt with selected Minnesota inbreds that excelled in standing ability. For these crosses the Minnesota inbreds used were A48 from Northwestern Dent, A2, A9, and A12 from Minnesota #13, and A39 from Rustler. Of these A39, A48, and A12 were classified as S, or strong stalk lines, and the remainder were classified as I, or intermediate in standing ability. These few lines were the best in standing ability among a great many originally selected from medium maturing Minnesota varieties.

Introduced lines used as one parent in crosses with Minnesota lines included A29(9-29), by the way of Wisconsin, but originally selected at Iowa from Osterland's yellow dent; A25(8-29), from Purdue yellow dent and an inbred from Holbert identified in our records as H. These three lines excelled in standing ability. They were also relatively desirable as inbreds in many other characters.

The method of breeding in this case was the pedigree plan which consisted of visual selection in the segregating generations during the process of selfing. A rather large number of inbreds from this program were tested for combining ability, and later the more desirable were used in double crosses. These in general were superior to Minhybrids 401, 402, 403, and 301 in yielding ability and agronomic characters. Certainly it was evident from extensive yield trials that they were some-

what more desirable as double crosses, and they replaced the first cycle hybrids eventually.

A part of more recently bred Minhybrids have some inbreds that are resistant to the first brood corn borer. Each of these new hybrids when introduced had been tested in comparison with previous available double crosses in extensive yield trials, and they proved superior in agronomic characters and also excelled in yielding ability. However, some inbreds from first cycle breeding, such as Wf9 and M14, are used very widely in commercial double crosses.

The Genetics of Heterosis

The hypothesis of dominance, or partial dominance, of linked growth factors as presented by Jones, and discussed previously, need not again be emphasized. It seems probable to many corn breeders that this often may be the more logical explanation of much of the hybrid vigor called heterosis in its overall application to both self- and cross-pollinated plants.

East (1936) presented a Mendelian concept of the interaction of alleles at a single locus to explain heterosis, where each allele had developed a divergent function. Some students of heterosis have concluded that East presented this explanation to take the place of the previous explanation of dominance of linked growth factors. This does not seem probable to the writer who prefers the viewpoint that the hypothesis of allelic interaction of factors was an addition to that already accepted of the dominance of linked growth factors. According to East's later hypothesis three or more alleles, A_1, A_2, A_3, etc., would have more effect when heterozygous, i.e. A_1A_2, A_1A_3, or A_2A_3, than in the homozygous condition, A_1A_1, A_2A_2 or A_3A_3. Hull's (1944, 1945) overdominance explanation was set up to account for the fact that the heterozygous condition may be more than the combined effect of both parents. In some cases in qualitative inheritance two pairs of complementary genes at different loci interact to produce a character, where either gene in a homozygous recessive condition inhibits character expression. Interaction of genes at different loci has been called epistasis. It seems probable that interaction could be obtained between allelic factors at the same locus.

Jones (1945a), Castle (1946) and Gustafson (1949) also have emphasized the probable importance of allelic interaction

as one genetic basis of heterosis. Later Jones concluded that the degenerative change he worked with was probably due to more than a single factor pair.

Sprague (1959) discussed types of gene action in relation to heterosis in corn. He assumed, "that the quantitative and heterotic attributes of interest are no less simple in their inheritance than the more adequately studied qualitative factors." He also thought it likely that all of the types of gene action reported for qualitative characters are also operative. The writer agrees that the conclusions are reasonable. One also may remember that quantitative characters are of great interest to the plant breeder and that a considerable part of accomplishments in plant breeding consist of improvements in quantitative characters. It seems, however, that present day knowledge in genetics leads to as sound approach in breeding for heterosis as for other quantitative characters.

The writer agrees in principle with Mather's (1955b) viewpoint. In self-pollinated species, selection is being made continually under normal conditions for the more desirable complement, or balance if one prefers that expression, of genes in a homozygous condition. In self-pollinated plants natural crosses occur with sufficient frequency in many cases to furnish the basis for new combinations of characters, but after the cross occurs there is a rapid approach to homozygosis as a result of self-pollination.

With intermediate species of crop plants, sometimes classified as often cross-pollinated such as sorghums, natural cross-pollination is more frequent than in the small grains such as wheat, oats, and barley, although self-pollination in sorghums is of considerably greater frequency than cross-pollination. Sorghums, however, have been bred in much the same manner as naturally self-pollinated plants. With the advent of an appreciation of the value of heterosis and with a mechanism for producing hybrid seed, F_1 sorghums are available that greatly increase yield and that rival hybrid corn in value.

Many of the students of the genetical basis of heterosis set up a background of the results of studies of hybrid vigor that may not seem entirely correct. Thus Mather (1955b) writes, "In the first place heterosis is a regular property of hybrids only in naturally outbreeding species." He writes also, "In inbreeding species they do not always exceed their homozygotes." Many years of research with corn leads the writer to conclude

that although all crosses of inbreds in corn are more vigorous than their inbred parents many F_1 crosses between inbreds are less vigorous than normal open-pollinated corn. It seems also that hybrid vigor, on the genetical basis, results from the fact that the F_1 has a more favorable complement, or balance of genes than the parents. In several species crosses of tobacco studied by East and Hayes (1912) the F_1 was much less vigorous than either parent. In some varietal crosses in tobacco heterosis was very great while other varietal crosses gave little or no evidence of heterosis. Numerous other workers have obtained similar results.

Other studies of inbreeding and cross-breeding have emphasized the effects on internal structure including chromosome behavior. Thus Reese (1955) studied meiosis in pollen mother cells of rye inbreds that previously had been self-pollinated for 26 generations, in contrast to similar studies made of F_1 crosses. Rye is known to be self-sterile to a rather high degree, although self-fertile lines can be obtained. The F_1 crosses reported by Reese produced chromosomes that were more efficient than in the inbreds, *i. e.*, they behaved more regularly during meiosis and without doubt also during mitotis, although this was not investigated by Reese. Previous studies of meiotic irregularities in inbred lines of rye and of other plants were reviewed by Putt (1954). He also presented evidence to show that some inbred lines were cytologically highly variable while others showed much less meiotic irregularity.

In studies with *Drosophila subobscura* by Smith *et al.* (1955), it was emphasized that hybrid populations are often less variable than inbred ones. This is a matter of common knowledge among corn breeders where it is known that an inbred line, even though highly homozygous, is more responsive to variations in climatic conditions than an F_1 hybrid, and in this case it does not seem probable that the result is due to chromosomal aberrations.

Pontecorvo (1955) started his discussion of gene structure and action in relation to heterosis by stating that heterosis may be interpreted in terms of gene action of two essential types, "One is that of interaction between nonallelic genes; the other that of interaction between alleles," and he ends his discussion by saying that the first steps for an understanding of heterosis, and also for rational utilization in plant and animal breeding and in marriage counseling, "should be a better understanding of gene structure and action." This seems equally true to the

writer for the application of plant breeding methods to the control of any complex, hereditary character of a quantitative nature. Certainly a knowledge of gene structure and function is basic. However, in corn breeding much has been learned regarding the breeding and utilization of hybrid vigor, and these principles furnish a basis for further improvement. Also the essential principles have been learned primarily by plant breeding technics that seem to be based on present day knowledge of genetics.

Brieger (1950) concluded, on the basis of a hypothetical statistical analysis of heterosis in maize, that the results can be explained in a satisfactory manner by the postulation of the, "existence of loci carrying special heterotic alleles which when heterozygous increase vigor." He emphasized his viewpoint that in South America, "we have at our disposal local or indigenous balanced populations, containing a large number of genes with a low survival when homozygous." This led him to suggest selection for a balanced population with South American maize. He cites as an example of the method a new type of sweet corn adapted to Brazilian conditions. After selection it maintained automatically its vigor, heterozygosity for heterotic gene pairs and uniformity.

In selection for such balanced populations Brieger proposed inbreeding for about three generations to eliminate recessive, undesirable characters and increase homogeneity of non-heterotic loci. During this period preference would be given to inbred lines less resistant to inbreeding. This would seem to mean the selection of less vigorous lines. Repeated and multiple crosses then would be studied to eliminate all inbred lines of low combining ability. The remaining multiple hybrids would be thrown together to form one breeding unit.

Experimental Studies of the Causes of Heterosis

Plant breeding studies not made primarily to determine the genetical basis of heterosis have given some indication of probable genetic causes. The definite and extensive relation, on the average, between the characters of inbred lines and the same characters in F_1 crosses seems to be in agreement with the hypothesis of dominant linked growth factors. One may include in these references also the very substantial positive correlation between the general combining ability of inbreds

as determined from test crosses and their specific combining ability in a series of inbred crosses with each other. While these studies seem to present evidence that heterosis may be explained to a large extent by the hypothesis of dominance, or partial dominance, of linked growth factors they do not preclude, or eliminate, other hypotheses such as over dominance or epistasis as other possible causes, in some cases, that are of importance in a complete understanding of the genetical bases of heterosis.

Richey (1927) presented a method of breeding called convergent improvement that has been discussed previously. One of its purposes, as stated by Richey, was to test the hypothesis of dominance of linked growth factors as a means of accounting for heterosis. This was first tested by Richey and Sprague (1931b). They found it possible to increase the yielding ability of inbred lines of maize while maintaining their performance in hybrid combination.

The convergent improvement method in brief can be summarized as follows: if a single cross A x B was outstanding in yield, it was proposed to backcross in several generations to the A parent, selecting during backcrossing particularly for characters of the B inbred that are lacking in A. After 2 or more generations of backcrossing and selection, selfed lines were produced and the more desirable selected and isolated. Similarly studies of improvement in the B parent were conducted as was outlined for the A parent. After improved lines of A and B were obtained these were tested in crosses in comparison with the original single cross, A x B. They found it possible to improve the inbreds and retain their yielding ability in crosses with each other. Murphy (1942) in similar studies found it possible to improve the inbreds in various attributes, and obtain in several cases, single cross hybrids that exceeded the original in yielding ability. Hayes, Rinke and Tsiang (1946a) used the method of convergent improvement in a double cross (11 x 14)(C23 x A374), where 11 and 14 are inbreds of Minnesota #13, and C23 and A374 were inbreds obtained from Holbert. The inbred lines of Minnesota #13 were much earlier than those from Holbert and were more susceptible to smut. In this study the Minnesota #13, inbred 11, was crossed with C23 and convergent improvement studied with both lines. Similar studies were made with inbreds 14 and A374. Recovered lines of inbred 11 were selected on the basis of their performance in crosses (imp. 11 x 14) compared with the single cross (11 x 14). Improved inbreds of 14, A374

and C23 were selected also in a similar manner. From single crosses between recovered lines the predicted performance of 862 double crosses was calculated. Of these, 46 were equal or superior in yield to Minhbrid 403. These 46 double crosses were compared in actual yield trials and ten of the selected doubles were equal to, or higher in yield than Minhybrid 403. Several yielded significantly more than Minhybrid 403. These results, as far as they go, furnish support for the hypothesis of partial or completely dominant genes in yield heterosis.

The studies of Murphy and Hayes *et al.* indicate, in some cases, partial dominance as a few crosses of recovered lines, where the cross of recovered lines exceeded that of the original cross, could be explained on the basis that the homozygous condition of one or more essential gene pairs resulted in a higher yield than when heterozygous.

Hull (1947) and Griffing (1950) used a regression analysis applied to a series of inbreds and their single cross combinations with special reference to yield. They calculated a second order of regression, "using the constant parent and the constant parent regression as variables." If the second order regression, b_2, was positive, dominance or partial dominance was considered to be of primary importance. If negative and of small magnitude, overdominance was considered to be of major importance. Analyses of several sets of data (Hull 1952) gave both positive and negative values of b_2, with negative values recurring in greater frequency.

Robinson, Comstock and Harvey (1949) calculated estimates of average degree of dominance for a series of characters, and obtained values for yield in excess of 1.0. While they concluded these could be due to overdominance it was stated that they could arise from close linkage of genes in the repulsion phase.

Sprague and Miller (1950) made a study of recurrent selection for specific combining ability to determine the relative importance of dominance or overdominance in heterosis. Sprague (1959) concludes the data obtained were in agreement with expectations under the dominance hypothesis. He concludes, however, "the results can be considered conclusive only after the completion of several cycles." Even then the results cannot be utilized to show what the genetic causes of heterosis are with other corn material.

Sprague and Russell (1956) presented a method to differentiate between heterosis due to dominance vs. overdominance.

They used two unrelated heterogeneous and heterozygous sources, called Lancaster and Kolkmeier, and practiced recurrent selection with a common inbred tester, Hy. Two cycles of recurrent selection were completed with each of the original sources. The selected material from the first cycle of recurrent selection, crossed with Hy, gave increased yields over the original for the crosses of Lancaster x Hy, and Kolkmeier x Hy. In the second cycle there was a slight but not statistically significant decrease in yield of the recovered Lancaster x Hy crosses in comparison with the first cycle. In the comparison of the results of the first and second cycles of selection for Kolkmeier in crosses with Hy, the second cycle of selection cross was superior at the 5 percent level of significance. Comparable data were obtained in 1955 for crosses of Lancaster x Kolkmeier and for first and second cycles of recovered Lancaster x recovered Kolkmeier. Substantial increased yield was obtained for the first cycle crosses over the original cross of Lancaster x Kolkmeier and for the second over the first cycle.

The hypothesis used was that if increased yields of recovered Lancaster x recovered Kolkmeier were obtained over the original cross in the first and second cycle crosses this would indicate a trend with respect to dominant alleles. If over-dominance was of primary importance as recovered Lancaster and recovered Kolkmeier became more alike in genotype, their crosses with each other would be expected to exhibit a decreasing trend in yield. The results obtained agree with the hypothesis of partial, or complete, dominance as a cause of heterosis.

Value of Heterosis

Dodds (1955) discussed hybrid vigor in plant breeding and seemed to conclude that Hayes, Immer and Smith (1955) have over-estimated the practical value of the results from utilizing heterosis. In the United States today, however, the back-yard gardener can purchase F_1 hybrid plants from the nursery florist for many different horticultural crop plants. Even though the plants are expensive, such F_1 hybrids are grown extensively. F_1 tomato hybrids are very widely grown in home gardens. F_1 hybrid sorghums appear to offer as much promise as hybrid corn. F_1 hybrids of onions and sugar beets have proven to be of considerable value. The utilization of heterosis in crop plants, largely cross-pollinated, can be accomplished on the

F_2 level and maintained in a constant state of heterozygosity. And also, as was emphasized by East and Hayes in 1912, crop plants propagated vegetatively utilize heterosis, called heterozygosis at that time.

Reference may be made to a recent review by Burton and Sprague (1961) entitled, "Use of hybrid vigor in plant improvement." Early history was not adequately reviewed, but they presented the work of Shull, and of Jones' double-cross plan of seed production. A considerable part of the summary was a discussion of the results of studies by Burton and co-workers where hybrid vigor was being utilized with Pearl millet, Sudan grass, Bermuda grass and Pensacola Bahia grass. These results of studies in recent years are cited as added evidence that heterosis will continue to be of extreme and wide importance to the breeder, and grower, of crop plants.

Physiological Manifestations of Heterosis

While most popular reviews of hybrid corn history have featured primarily the increased yielding capacity of the better hybrids, the improvement in other characters is of equal and perhaps even greater significance than increased yield. Ability to withstand lodging, resistances to pests, uniformity of maturity, availability of high quality seed, etc., are very valuable results from present-day methods of corn breeding.

An understanding of the reason why hybrid corn is of such great value incluees a knowledge of many characteristics of hybrid corn in comparison with open-pollinated corn. Valuable contributions to these phases were made by Kiesselbach and numerous co-workers. Other studies that seem of less general interest will not be reviewed.

Kiesselbach (1926a) reviewed many of the experiments on the immediate effect of foreign pollen on the weight of hybrid kernels and presented extensive data. Some writers, such as Lyman Carrier, concluded that this was one cause of difficulty in obtaining accurate comparisons in varietal trials, while others found that the effect was of little or no importance. Kiesselbach (1960a) made a further review of the work of others with special reference to Xenia effects on kernel weight in corn, presented new data, and summarized previous data of himself and co-workers. In some cases there were marked effects of the source of pollen on the development of kernels of inbreds.

This was very evident with two inbreds Wf9 and R4. Thus "Wf9 pollen increased the kernel weight of R4 by 46.6 per cent, whereas R4 pollen decreased the kernel weight of Wf9 by 17.6 per cent." The acre-yield of sweet corn and waxy corn was increased by an average of 27.2 per cent by Xenia when outcrossed with dent. However, it does not seem for hybrid strains of dent corn that off-pollination, as a rule, is of sufficient importance in yield trials to greatly modify the results of the trials.

Kiesselbach also concludes, "that hybrid vigor of an F_1 progeny is not related to initial difference in size of seed planted." It is evident that this refers primarily to inbreds or hybrids that have good capability of seed production and that exhibit what one calls normal reaction.

Kiesselbach (1922) presented data on the histological effects of inbreeding and crossbreeding. Increased plant size due to crossing inbreds was attributed to a 10.6 per cent increase in cell size and to an 89.4 per cent as a result of increases in cell numbers. Studies of transpiration (1926b) of selfed lines, hybrids, and open-pollinated varieties were made, using as a source of material Hogue Yellow Dent and Nebraska White Prize. Selfed lines often differed very widely. In a study in 1924, with selfed lines, transpiration per gram of moisture-free ear corn varied from 448 grams to 1,013. In a two-year comparison of open-pollinated Nebraska White Prize with selfed lines and F_1 hybrids of lines from this variety, the selfed lines transpired an average of 900 grams water per gram of dry ear corn, the F_1 hybrids gave average readings of 443 grams, the F_2 hybrids 514 grams, and the original variety 470 grams.

Kiesselbach and Weihing (1935) also compared the root systems of several parental inbred lines, including Ind. B2, Ill. A, Iowa 197, and Iowa 420, with the two F_1 crosses (Ind. B2 x Iowa 197), and (Ill. A x Iowa 420) and obtained the averages given in Table 19 for main roots.

These results show that heterosis leads to greater root development as would be expected. The reduction of root branches per inch in hybrids in comparison with their inbred parents is in agreement with previous conclusions that the large effect of heterosis is due to increased number of cells in various parts of the plant.

Hsu (1950) in Minnesota studied the effect of two pairs of dwarf factors in their homozygous dominant and recessive conditions and also when heterozygous in near isogenic, homozygous,

Table 19 Comparison of root development of inbreds and their F_1 and F_2 crosses

Material	Depth of Penetration	Combined Length of Main Roots	Maximum Spread	Root Branches per inch
	ft.	ft.	ft.	
Inbreds	3.2	328	3.1	13.6
F_1	4.6	476	3.6	12.5
F_2	3.9	396	3.1	12.8

and highly heterozygous backgrounds. Mesocotyl length was taken under controlled laboratory conditions as made available by Professor Ernst Abbe of the Botany Department, University of Minnesota. The different genetic progenies were grown also under favorable field conditions. Dr. Abbe collaborated with the writer in advising Hsu in all phases of the study. It was evident that the different genetic backgrounds greatly affected the extent and rapidity of mesocotyl growth. That is, "the types of response of inter and intra allelic factor interaction are without doubt dependent upon both external and internal environment." (Hayes, 1952)

Whaley (1952) discussed the "physiology of gene action in hybrids" in a very complete and illuminating manner. In relation to his own studies of corn inbreds and single and double crosses he concludes, "that the hybrid advantage lies in the more rapid unfolding of certain metabolic processes." He summarized the reactions of corn inbreds and hybrids under controlled conditions in the laboratory, to radioactive phosphorus, and refers to the studies of nitrogen metabolism by Harvey (1939) and Burkholder and McVeigh (1940). His conclusion is quoted as follows, "All the evidence seems to indicate that the greater absorption of minerals by heterotic hybrids can be referred to better development of root systems in the hybrids, probably also to the presence of more efficient transport systems, and to a generally higher level of metabolic activity." Whaley discusses also the role of specific substances in heterosis. He refers to the researches of Hoffer (1926) who found that iron and aluminum content was lower in the ash of hybrids than in inbreds. The amount of absorption of iron and aluminum was markedly different in different soil types but under various conditions the vigorous hybrids tended to absorb less than vigor-

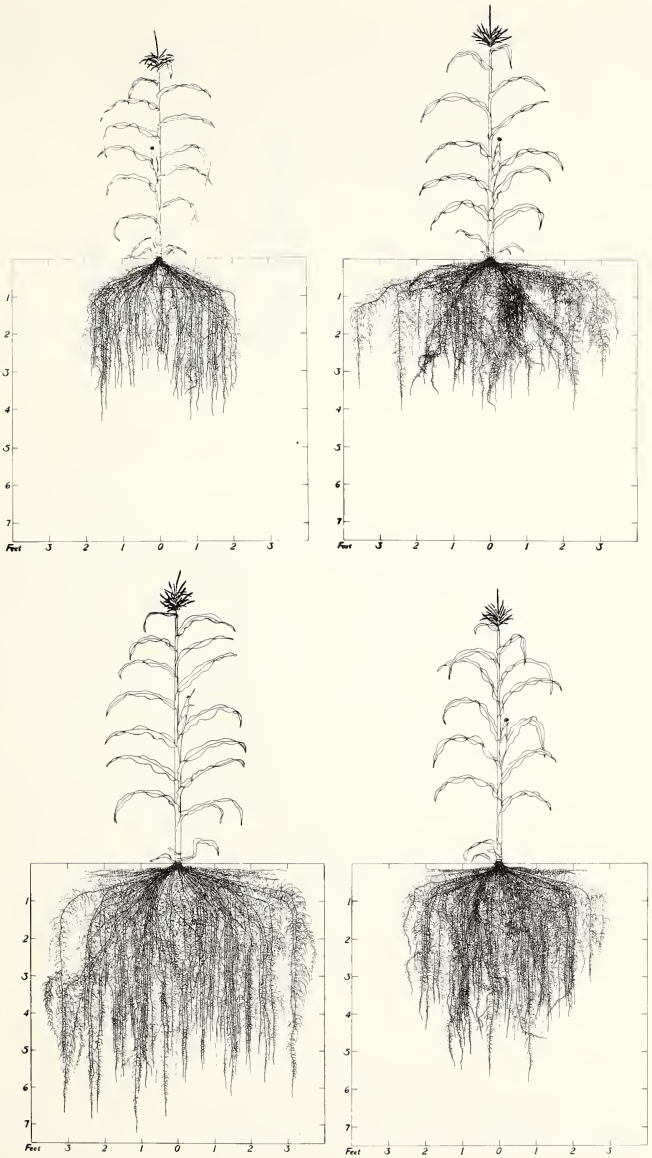
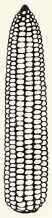


Figure 12 Representative plants of inbred parents, F_1 and F_2 crosses between them. Upper left, Ill. A; upper right, Iowa 420; lower left, F1 and lower right, F2. Approximately 25% of the branch roots are shown.

(After Kiesselbach and Weihing, 1935)

ous inbred lines. In some cases it seems evident that heterotic hybrids have the ability to synthesize certain growth substances which the hybrids either cannot synthesize or cannot synthesize as well. It seems evident that these capabilities as outlined in greater detail by Whaley are under genic control.

Chapter 10



GENETICS AND CYTOGENETICS OF CORN

Introduction

A discussion of hybrid corn history would seem incomplete without reference to the extensive and comprehensive experiments in corn genetics and cytogenetics. It seems fair to conclude that studies with corn have been of greater importance in relation to present-day viewpoints of genetics and cytogenetics than those with any other organism except Drosophila. This was one reason for brief reviews of early genetic studies of corn by East, Emerson and the writer, referred to in relation to early investigations relating primarily to hybrid vigor.

There will be no attempt in this review to present a very comprehensive summary of the many investigations in genetics and cytogenetics of corn. Various comprehensive reviews will be referred to and students may consult these reviews and original research papers.

Linkage Studies

For many years Emerson and his co-workers led in studies of the genetics of corn. The research memoir by Emerson and others (1935) consisted of a comprehensive summary of linkage studies carried out prior to that date. The linkage map utilized by Hayes, Immer, and Smith (1955), prepared largely by Dr. C. R. Burnham, included data from previous summaries by Emerson *et al.* (1935). Only those genes were included by Burnham for which the order was relatively well established. These consisted of 20 genes in chromosome 1, 12 genes in

chromosome 2, 14 genes in chromosome 3, 13 genes in chromosome 4, 8 genes in chromosome 5, 7 genes in chromosome 6, 13 genes in chromosome 7, 3 genes in chromosome 8, 11 genes in chromosome 9, and 10 genes in chromosome 10; a total of 103 genes. Approximate locations of the centromere were given also.

It is of interest to point out that each of the individual 10 chromosomes have been identified cytologically as observed under the microscope. Also each of the 10 linkage groups has been placed in one of the 10 chromosomes, and the orientation of the genes concerned has been determined by linkage studies. In a considerable number of cases the actual location of a gene in a definite location of a particular chromosome has been determined by cytogenetic means.

Cytogenetics

The literature on cytogenetics of maize is very extensive. Creighton and McClintock (1931) first demonstrated the correlation between genetic and cytogenetic crossing over. Rhoades and McClintock (1935) and Rhoades (1955) presented extensive reviews of the literature on chromosomal aberrations. The occurrence of triploidy was discussed by McClintock (1929), and Randolph (1932) studied the production of triploid and tetraploid maize by heat treatments. In a study of tetraploid stocks Gillis and Randolph (1951) found that the relative frequency of bivalent associations increased markedly during a ten year period while the stock had been maintained by the selection of the most fertile plants.

Chase (1949) discovered plants with a monoploid set of 10 chromosomes arising chiefly from the parthenogenetic development of the unfertilized egg. The progeny of such self-fertilized plants are homozygous diploid and Chase suggested the development and utilization of such inbred lines as a breeding procedure. Thompson (1954) studied the combining ability of homozygous diploids of corn relative to lines derived by inbreeding. He found no significant differences between the combining ability of homozygous diploids and of inbred lines from the same source. He wrote that there seemed to be no, "selective advantage as measured by combining ability of homozygous diploids for the population studied."

There have been numerous studies of translocations in

corn. Longley (1961) reported 1003 chromosome translocations, the chromosomes involved, and also in most cases the points of breakage.

Burnham (1946) suggested a multiple translocation method of establishing homozygous inbred lines. Considerable progress has been made in the development of a tester in which all chromosomes have been translocated, essential for the production of inbred lines, and which will form a ring of 20 chromosomes during meiosis as in *Oenothera*.

Inversions are of various types and genetic crossing-over is suppressed. Dobzhansky and Rhoades (1938) suggested the use of inversions to locate favorable genes, and Sprague (1941) carried out a study that showed the method was of value.

Mutation

The writer (1917) studied mosaic pericarp pattern color. Somatic mutation was consistently rather frequent in the progenies of a particular cross but at that time no suggestion was made regarding the probable cause.

Stadler (1930a, b) reported the mutation rate for 8 genes affecting the development of endosperm characters and found the *R* locus, which is essential to the development of anthocyanin pigment in the aleurone cells, and also pigmentation in seedling and plant characters, to have the greatest frequency of spontaneous mutation, and the gene for waxy endosperm, *wx*, to have the lowest frequency of mutation among those studied. Stadler (1928) presented the first evidence for the production of induced mutations in crop plants by X-rays and radium.

Rhoades (1941), McClintock (1953) and Brink and Nilan (1952) presented evidence that certain genes were the cause of increased mutation rates in other genes. Studies of gene control of mutations eventually may lead to the control of mutational rates when sufficient information becomes available.

Chlorophyll Development

Many investigations of the genetics of chlorophyll abnormalities have been made and a general review was presented by Hayes et al. (1955). It is evident that there are several genes in nearly every chromosome that are responsible for chlorophyll

development. Some of these when recessive modify chlorophyll development in the seedling plant, others affect its development in the mature plant, and still others affect chlorophyll development in both the seedling and mature plant stages. There are probably over 100 genes known that affect chlorophyll development either in the seedling or mature plant stages and it seems safe to conclude that over 100 genes, therefore, are necessary for normal chlorophyll development. Complexities of this nature may give some idea of the possible or probable complex nature, in some cases, of the genetics of heterosis.

Quantitative Characters

For many quantitative character differences it is relatively easy to demonstrate that the character appears to be dependent upon the interaction of many factors. However, their number and nature often are difficult to determine. Where dominance is complete, and the factors are of like nature, and additive, the expected type of segregation may be determined by the expansion of the binomial $(3 + 1)^n$, where n is the number of allelic factors. When the heterozygous condition of a factor gives half the effect of the dominant homozygous condition, and there is a cumulative effect of one factor on another, and all factors are of equal value, expected ratios in F_2 may be obtained by the expansion of the binomial $(1 + 1)^{2n}$ where n also is the number of factors concerned.

Lindstrom (1931) showed that factors for row number were linked with the gene pair for cob color. An interesting and very illuminating study was presented by Emerson and Smith (1950). Different strains that bred relatively true for 12-rowed ears were isolated. Intercrosses were made and all but one cross segregated for row numbers.

It seems apparent to the writer that in most instances where quantitative characters are governed by genes, it is not feasible to determine the number, nature and types of factor interaction that govern quantitative inheritance. Heterosis may well be dependent upon similar types of factor interaction.

The well known experiments (Woodworth and others, 1952) of continuous selection for high and low protein and high and low oil at the Illinois Station illustrate the complexity of inheritance of quantitative characters. The methods used are summarized in some detail by Hayes, Immer and Smith (1955). There was

continuous progress through selection, without definite control of pollination, for high oil content, and for high and low protein, for a period of 50 generations. No very significant change occurred for low oil content from the 30th to the 50th generation. Reverse selection after 48 generations was started to test whether heritable variability for each of the chemical components still remained. Recently Leng[1] (1961) has reported the results of 13 generations of reverse selection. He states, "The rates of response were comparable to those observed in the early generations of the original selection experiment." It seems probable as suggested by Leng, that the release of genetic variability through continuous recombination accounted for the responses to selection that were obtained.

Disease Resistance

Hayes, Immer and Smith (1955) summarized studies of the inheritance of reactions to smut. Through the use of chromosome interchanges it was found by several investigators, Burnham and Cartledge (1939), Saboe and Hayes (1941), and Saboe (1942), that there are many loci for reaction to smut in the crosses studied. The loci were different in the different crosses. Various researchers have found it relatively easy to isolate smut-resistant lines by selection in self-fertilized lines that give satisfactory resistance under various environmental conditions. With open-pollinated corn smut often had a marked effect on yield as most normal varieties were rather susceptible. Many hybrids today are moderately resistant to smut and it is not uncommon to hear a plant pathologist say that the smut disease of corn is of little practical importance. It is known under greenhouse conditions and with artificial inoculation that there are races of smut and that an inbred strain may be resistant to one race and susceptible to another. As smut resistant corn usually reacts the same way in different seasons and locations to the smut organism it seems that a generalized type of resistance is produced by various combinations of widely different sets of genes.

Jenkins and others (1957a) studied the inheritance of resistance to leaf blight, caused by *Helminthosporium turcicum*,

[1]In Agronomy Abstracts, Published by the American Society of Agronomy, Madison, Wisconsin, 1961.

by means of translocations. Resistance was associated with 8 arms of chromosomes of Mo 21A and 6 arms of NC 34, and susceptibility was associated with 2 arms of Mo 21A.

Richey (1950), Hayes *et al.* (1955) and Ullstrup (1955) briefly reviewed many other studies of disease resistances in corn. Wellhausen (1937) made an interesting study of reaction to bacterial wilt. He explained the results obtained by three genes. When all were dominant a high degree of resistance was obtained. When a single factor was dominant even though the other two were recessive, either homozygous or heterozygous, a certain degree of resistance resulted.

Several investigators have studied resistance to soil-inhabiting fungi. There was evidence of the inheritance of resistances but the results were not placed on a definite genetic factor basis.

Under Minnesota conditions ear, root and stalk rots are due primarily to two pathogenic organisms, *Giberella Zea* and *Diplodia Zea*. Extensive studies have been made of the reaction

Figure **13** Disease nursery at University Farm, St. Paul 1, Minnesota for the study of reaction to root and stalk rots under field conditions and to collections of root and stalk rot pathogens. Note the apparent resistance of lines in the foregound. (Courtesy of R. D. Wilcoxson, Department of Plant Pathology and Plant Physiology, Institute of Agriculture, University of Minnesota)

of corn varieties, inbred lines and crosses to pure cultures of these organisms. It is evident that physiological races of each organism are present and that a particular inbred may be resistant to one race and susceptible to another. Selection, however, under field conditions, has led to the development of resistances and to partial control (See Fig. 13). Reece (1949) proved conclusively that resistance to single spore isolates of both organisms was definitely inherited and in a complex manner. It is generally conceded that root, stalk and ear rots usually cause significant reductions in yield. The organisms gain entrance through wounds and it is difficult to differentiate completely between the effect of the European corn borer and root worms and the pathogenic organisms that accompany these insect pests.

Leaf blights due to various organisms have been studied, under partially controlled environmental conditions in some cases, and it has been found possible by Jenkins and Robert (1952) to isolate resistant or partially resistant lines. It was concluded by Jenkins *et al.* (1957b) that there were a rather large number of major genes for resistance or susceptibility. Jenkins, Robert and Findley (1954), as reviewed by Sprague (1959), reported the effectiveness of recurrent selection for resistance to *Helminthosporium turcicum,* leaf blight. Selection was more effective during the first two cycles.

Reaction to Insects

Richey (1950), Dicke (1955) and Hayes *et al.* (1955) reviewed studies of resistances in corn to insect pests. Painter (1951) made an excellent review of insect resistances in crop plants. Differences in reaction in corn were observed by numerous investigators including studies of reactions to corn ear worm, grasshoppers, white grubs and southern corn root worm. With continuous corn culture, which has been recommended by some agronomists, the corn root worm in some cases is rapidly becoming a more severe pest in corn fields. Resistances of different varieties and hybrids have been noted to the southern corn root worm by Bigger and others (1941).

Differential reactions of lines and hybrids to the European corn borer have been observed by many investigators. Numerous researches have been reviewed briefly in the general reviews referred to. Definite resistances have been observed

and studied for reaction to the first-brood larvae and there are differential tolerances to the second-brood borer of a less definite nature.

Cooperative studies have been made by entomologists and plant breeders at Minnesota for reaction to leaf feeding, and overall injury by the first-brood larvae. In these studies larvae were placed on each individual plant and by this method resistant and susceptible plants and lines were isolated. Resistant lines for use in crosses were obtained also from other investigators. Detailed studies were made and the individual plants of inbred, F_1, F_2 and back-cross generations were classified for their reactions. In these studies (Fleming *et al.* 1958), the F_1 was in some cases as resistant as the resistant inbred parent. In other crosses reaction was intermediate between that of the parents. Segregation was rather satisfactorily explained on a two factor basis. If further studies give comparable results partial resistance in single- or double-cross hybrids can be obtained by using a resistant parent as one parent of the single or of the double cross.

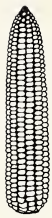
Ibrahim (1954) used chromosomal interchanges to study the inheritance of resistance to the European corn borer as a phase of the cooperative study at Minnesota. A411, a corn borer resistant line which was selected in F_6 from the cross of A131 with Oh. 7, the source of borer resistance, was used as a parent in the crosses. The conclusion was reached that the resistance of A411 is a result of "at least one gene in the long arm of chromosome 3, one in the long arm of chromosome 4, and probably another in the long arm of 5."

Conclusion

Genetical and cytogenetical studies are essential to a determination of the genes that cause resistances and susceptibilities to plant pests, to manner and reaction to various environmental factors, to the mode of inheritance of yielding ability including utilization of food substances by the plant, to reactions to sunlight, carbon dioxide content of the air and to drought and humidity. The broad reasons why an inbred or hybrid responds favorably or unfavorably to particular conditions of moisture, fertilization and sunlight are becoming better understood through combined studies of heredity and environment. When the manner of inheritance of yielding ability

is conditioned by many genes, their reaction and interaction, the breeder utilizes this information to determine what method of breeding seems most reasonable. At present the utilization of heterosis which in itself seems one phase of quantitative inheritance has been obtained by an application of principles learned by extensive and intensive cytological, genetical and breeding studies.

It seems evident that resistances to disease organisms such as smut, or to larval feeding of the first-brood larvae of the European corn borer, would under conditions of infection, or infestation, add to the desirable characters of a hybrid and in this way be of increased value in breeding for heterosis. It is known, for example, that resistance to the first-brood larvae of the European corn borer is a partially dominant or completely dominant character in crosses between resistant and susceptible lines. However, there seems reason for believing also that all parents of a single, or double cross, could be provided with the necessary factors, or genes, for resistance and thus eventually eliminate the use of heterosis for reaction to disease and insect pests.

Chapter 11  TECHNICS IN THE PRODUCTION OF HYBRID SEED

Introduction

With the development by corn breeders of double crosses, adapted to different conditions, a complete set of new problems faced the producers of seed. This may be appreciated by contrasting methods of seed production of open-pollinated corn varieties used formerly with that of hybrid seed production of today.

During the many years after the discovery of America corn played a major role in the economy of American agriculture. With the settlement of new areas by early colonists new varieties of corn were developed as needed for new environmental conditions. There often is no clearly recorded history of these developments, although it is generally appreciated that improved, better adapted varieties played a major part in the expansion of corn acreage in the United States.

When one speaks of the Corn Belt there are different ideas of what is meant. Certainly in the days prior to 1900 Minnesota and other important corn growing states in the North Central region would not have been included. In Minnesota corn now is the major crop, and in recent years Minnesota has been in the third to fifth place in total production of grain, often exceeded only by Iowa and Illinois. The varieties and hybrids grown in Minnesota have been selected for earlier maturity than hybrids adapted to much of the Corn Belt area.

Corn is nearly 100 per cent cross-pollinated and selection has been based primarily on the best combination of characters in a heterozygous condition. A brief history of early varieties of corn grown in Minnesota may serve to illustrate the nature

of breeding problems in the early days, although the details of the story would be different for widely differing climatic conditions.

The story of Minnesota #13 corn often has been told. As I learned it, Professor Andrew Boss was sent by Willett M. Hays in 1893, at that time Minnesota's great agricultural leader, to St. Paul where a small amount of yellow dent corn seed was purchased. At this early period Willet M. Hays was recognized as one of the plant breeding leaders in the United States. It is usually appreciated also that he was a great theorist but somewhat less capable, or less interested, in carrying out the necessary studies to prove the truth of his hypotheses. He is credited as being one of the first to appreciate the value of and to introduce the method of individual plant selection about 1900 with self-pollinated crop plants.

After testing new introductions of corn for several seasons, the better producing types were increased and distributed. Thus, several years after Boss purchased the sample of yellow dent corn in St. Paul, it was introduced under the name, Minnesota #13. It has spread widely and has been grown in many foreign countries.

Seed companies, like the Northrup King Company, played an important role in the distribution of adapted varieties, including selections of the varieties, Silver King, Rustler, Northwestern Dent, and varieties of flint such as Longfellow and King Philip. Some of these were strains selected and propagated by leading farmer seed growers. Many illustrations could be given. For example Clarence Blanchar, Fox Lake, who for many years was a leader in the Minnesota Crop Improvement Association, and who was responsible in a large measure for added support for crop breeding studies at the Minnesota Station, grew a strain of Silver King, which not only was sold by him to other corn growers, but which was sold also by the Northrup King Seed Company. Silver King also was grown, selected, and distributed by the Southern Experiment Station at Waseca.

Strains of Minnesota #13, and of other varieties were selected by growers of the Crop Improvment Association. Among strains of Minnesota #13 one might mention the Haney strain selected for early maturity in the Red River valley, the Lein strain for the St. Cloud region, and Kalmoe's, a longer and heavier eared type with a reddish blush to the pericarp for west central Minnesota. Then two Experiment Station strains were produced and distributed by the Central Station at St. Paul and

the West Central Station at Morris. This Morris strain, selected from vigorous plants in perfect stand hills surrounded by corn on four sides, and not selected too closely for ear type, was outstanding in yield trials conducted early in the nineteen twenties.

During all of these early years many farmers saved their own seed. In seasons like 1915 and 1916, when the writer first lived in Minnesota, there were severe early frosts in the fall before corn was completely matured. A great deal of attention, by Experiment Station and Extension workers, was focused on aiding in finding sufficient seed supply for the next year's crop. Such early freezes were a great hazard to the corn grower as much of the seed often was of low and weak viability the following year. New seed introduced from other areas of the Corn Belt was often a hazard also, because it produced a crop that matured too late for the average Minnesota season.

Production of Hybrid Seed

With the advent of hybrid corn, seed production was on an entirely different basis. Each double cross has four inbred parents that must be maintained. Two of these are used to produce a single cross used as the female parent of the double cross, and the other two are used to produce the single cross used as the male parent. These two single crosses are grown in alternate rows in isolated plots, as explained previously, and the female single cross is detasseled before its silks appear. The plants of the female are pollinated by wind-borne pollen from the male rows of the single cross parent. The seed produced on the female is the source of seed for hybrids planted by the farmer.

Because of the extra work of producing hybrid seed, and the added costs of essential procedures as compared with seed production of open-pollinated corn varieties, a great deal of research has been carried out on all phases of seed production, including processing, drying, grading, and treating of seed. For the most part special machinery is now used for each of these steps.

Thus since the development of hybrid corn procedures, the corn grower obtains seed that is rather uniformly of high quality. Such seed not only excels in characters selected for by the breeder, but also has excellent viability, is graded uni-

formly which aids in machine planting, and is treated with various chemicals to aid in the control of seed-borne diseases. In addition, therefore, to better heredity, which in itself is of fundamental importance, there is always sufficient seed available to the farmer that, if properly planted, insures good stands of corn under normal conditions.

While Experiment Station researches have played a part in basic studies, such as those carried out by Harrison and Wright (1929), who devised one of the more satisfactory methods of artificially drying seed, many of the developments that have led to corn seed of high quality have resulted from studies made by commercial producers of hybrid seed. Not all of the increase in yields of hybrid corn over open-pollinated corn is the direct result of improved heredity. A considerable part of the credit for increased yields of hybrid corn is due to the availability of seed of vigorous viability.

One of the problems of seed production of hybrids consists of the maintenance of the parental inbreds and the production of sufficient seed of single crosses for use in double-cross seed plots. There are different ideas of the better methods of carrying out the various operations.

Studies under support of the Rockefeller Foundation in Mexico are of considerable interest in relation to the problem of maintenance of the inbred lines. In attempting to develop hybrids in as short a time as possible they produced double crosses from inbred lines that had been selfed only for a single generation. One such double cross has been grown commercially rather extensively in Mexico. It has yielded about as well as similar double crosses made from inbreds of the same origin that were selfed and selected for the usual number of selfed generations that is commonly the practice for double-cross hybrids grown extensively in the Corn Belt.

It is a common practice to self for about five generations before using selected inbreds in hybrid production. Continued selfing until there is a close approach to complete homozygosis usually leads to a gradual reduction in the vigor of the inbred. Thus, one of the inbred lines from Leaming, from East's studies, was called 1-6. It is a tall, dark green inbred that stands up well. Its great weakness as an inbred is low pollen production. It is not known to the writer when this characteristic was first evident but during the period that this inbred was handled by him the weakness of low pollen production was certainly not as evident as in later years at Minnesota when this inbred was grown. Jones has emphasized this characteristic of 1-6.

Figure **14** The ear shoot bearing the female flowers may be covered with a glassine or vegetable pachment bag before the silks appear. During the process of producing inbred lines each ear-row usually is the progeny of the seeds of a single plant that was self-pollinated the previous generation. The more promising rows are selected, and the better plants within the row then are self-pollinated. Visual selection consists of selecting plants that appear to have the ability to withstand lodging and that appear to excel in freedom from abnormalities, that bear leaves that remain green to maturity, that are not severely injured by diseases or insect pests, that produce vigorous plants and ear and tassel shoots with plenty of silks and ample pollen. Continued selection in self-pollinated lines is carried out for about five years and the desirable, uniform appearing inbreds then selected and tested for their desirability as parents in crosses. (Courtesy of H. Kendall Hayes, Jr., Hybrid Corn Division, Cargill Inc.)

The writer and associates have been constantly searching for vigorous inbred lines. In several cases inbred lines that seemed remarkably vigorous have appeared. From the results of further selection, under self-pollination conditions, it has seemed probable that most of these that were studied resulted from outcrosses. A particular case, however, where this was not the cause of the apparent vigor may be cited. This was an inbred of purple aleurone flour corn that appeared to be very uniform with vigorous plant growth, with a plant of dark green color, and a desirable tassel and ear. After about six generations of selfing this inbred suddenly developed a tendency to low pollen production that was correlated with a strong tendency for the glumes of the male flowers to remain closed and in this manner prevent sufficient production of viable pollen. In other cases a seemingly vigorous inbred may gradually, on continued self-pollination, approach a condition where ear production is not satisfactory. Results of this nature have occurred in inbred lines on continued self-pollination. Mangelsdorf (1952) has emphasized the importance of what he called bottleneck genes that when homozygous greatly depress yielding ability and may be responsible for modifying the extent of heterosis in crosses.

Inbred Seed Production in Minnesota

These difficulties are the main reason why a special procedure was adopted at Minnesota in maintaining inbreds for use in double crosses, as was presented by Borgeson and Hayes (1941).

Hand crossed and selfed seed of all inbred lines needed in the corn program is planted each year in foundation plots at both the Southern and Central Stations. By planting at two locations, and at several different times at each, the hazards are partially overcome. Sufficient selfed ears are produced by hand pollination to provide the necessary seed for the following year in the plots where single crosses are produced.

All off type plants are rogued from the selfing plots before pollination. In many cases as high as 1000 self-pollinated ears are produced for an inbred that is used extensively in double-cross hybrids. Before the ears of each inbred are shelled, they are examined carefully both before and after drying by those in charge of seed increases, and when desirable, by one or more of the corn breeding staff that are most familiar with the charac-

Figure 15

The tassel bagging operation illustrated. Self-pollination consists of placing pollen from the tassel of a plant on the silks of the same plant. A pollen grain germinates, sending out a pollen tube through the silk which bears two male sexual cells. One of these unites with the egg at the base of the silk to form the embryo, the other unites with two polar nuclei of the female gametophyte to form the kernel's endosperm. After pollination the ear shoot is covered to protect it from foreign pollen usually using the tassel bag. Hand crosses can be made by pouring pollen from one plant, or plants of the male parent, over the ear shoots of the plant or line to be used as the female parent. (Courtesy, Hybrid Corn Division, Cargill, Inc.)

teristics of the inbred. At this time approximately thirty individual representative ears are selected from each inbred line. The more desirable ears are selected, but these are not closely selected for any one type. There is in this case an attempt to maintain as great variability as feasible without great modification of the characters of the inbred. The balance of the selfed seed is bulked for use in producing single crosses.

The following year short "ear-to-row" cultures from 20 to 30 selfed ears of each inbred are planted. In case any of the progenies are off type, those cultures are discarded, although this is an unusual and very infrequent occurrence. Hand crosses are made between the individual ear cultures of the nature, where the cultures are numbered within the inbreds as 1, 2, 3, 4, etc., of 1 x 2, 2 x 3, 3 x 4, etc. These crosses are grown in ear-to-row plots the following year and are examined at harvest time. If any culture, such as cross 1 x 2, appears to deviate in a marked degree from the inbred in plant or ear characters at harvest, the cross in which that culture is used as one of the parents is discarded. The seed of the remaining crossed ears is bulked and used the following year to further propagate the selfed line, in which hand-selfed ears are produced for use in single crosses.

The method outlined here has been explained at field days held at the Southern Experiment Station. On one such day after explaining the details a member of the Pioneer Hi-bred Seed Company told the writer that they used a similar plan.

If this plan, or a similar one, is used with inbreds that have not been selfed for more than five or six generations, it seems probable that each inbred can be maintained in a relatively stable condition. It also has been concluded that inbreds handled in this manner often appeared to improve in general characteristics and that an inbred can be maintained on a somewhat more vigorous basis than when its first extensive propagation was started. As carried out the method seems to be a form of recurrent selection for visual characters.

Male Sterility

In recent years methods have been devised to eliminate, to a large extent, the detasseling operation by the use of male sterility. No attempt will be made to review in detail the development of methods that made possible the utilization of cyto-

Figure **16** When the silks appear they can be seen through the glassine or vegetable parchment bag, and at this time a tassel bag is placed over the tassel, to collect pollen, at least 24 hours before pollination. After 24 hours any foreign pollen that accidentally was included in the pollination bag will no longer be viable. (Courtesy, Hybrid Corn Division, Cargill, Inc.)

plasmic-genetic male sterility in corn. Later with explanation of breeding methods, backcross methods will be illustrated to show the steps usually followed in adding the cytoplasmic condition to an inbred without greatly modifying its genotype. Also the steps will be outlined of adding a restorer gene to an inbred which when heterozygous lead to the production of fertile pollen even in the presence of cytoplasmic-sterile cytoplasm.

Sears (1947) pointed out three types of male sterility, called A, cytoplasmic-genetic; B, cytoplasmic; and C, genetic. Corn has the cytoplasmic-genetic type.

In the absence of the dominant condition of genetic factors for restoring pollen production all of the offspring of a cross of cytoplasmic sterile (female) x cytoplasmic fertile (male) will be sterile. When, however, the cross is of cytoplasmic (female), with recessive restorer genes, by a male that has cytoplasmic fertile or sterile cytoplasm, but carries genes for pollen fertility, the immediate offspring will produce fertile pollen.

When cytoplasmic sterility alone is present and double-cross seed is produced by a cross of cytoplasmic sterility x cytoplasmic fertility, it is necessary to blend seed of a similar cross that lacks sterile cytoplasm.

Single- and Double-Cross Seed Plots

For each double cross it is necessary to produce three crosses, two single crosses, and the double cross produced by crossing the parental single crosses. Each of these crosses is produced in an isolated plot. Seed for the female parent of each of the two single crosses is used to propagate that cross. The single-cross seed is used to plant the double-cross seed plot.

The general methods used were described in Chapter 1 and explained partially by Figure 1.

The addition of cytoplasmic-genetic male sterility to female inbreds, or female single crosses, may be carried out to obviate detasseling. The incorporating of restorer genes to one, or both, of the male inbreds used to produce single-cross male parents of the double-cross plot, restores pollen production of the double cross grown by the farmer who produces hybrid corn.

Chapter 12 BREEDING METHODS

Introduction, Types of Crosses, Selecting the Inbreds, Use of Inbreds in Hybrids

Introduction

A review of the development of hybrid corn would be incomplete without discussing breeding methods. While the writer has read most, if not all, of the published research and breeding papers no attempt will be made to review each of these in detail. Comprehensive reviews have been published. These include Hayes and Immer (1942), Richey (1950), Hayes, Immer and Smith (1955) and Sprague (1955, 1959). These reviews present a summary of important steps in the development of hybrid corn and list the more important research, breeding and other phases of the problem. The student interested in corn breeding may consult these reviews, and the original researches when desirable, to obtain more complete familiarity with the history of hybrid corn and the present status of the problem.

The development of desirable inbred lines to use in hybrids has been discussed previously. Further discussion will be necessary in relation to various breeding procedures, and further research information will be reviewed in relation to the results of breeding studies that are summarized.

Types of Crosses

The parental lines are maintained as inbreds. If these are designated, for illustrative purposes, as A, B, C, D, etc., the final product is one of the following types of combinations:

1. The single cross. Illustrated by any combination of two inbreds, *i.e.*, A x B, A x C, B x C, etc. Seed produc-

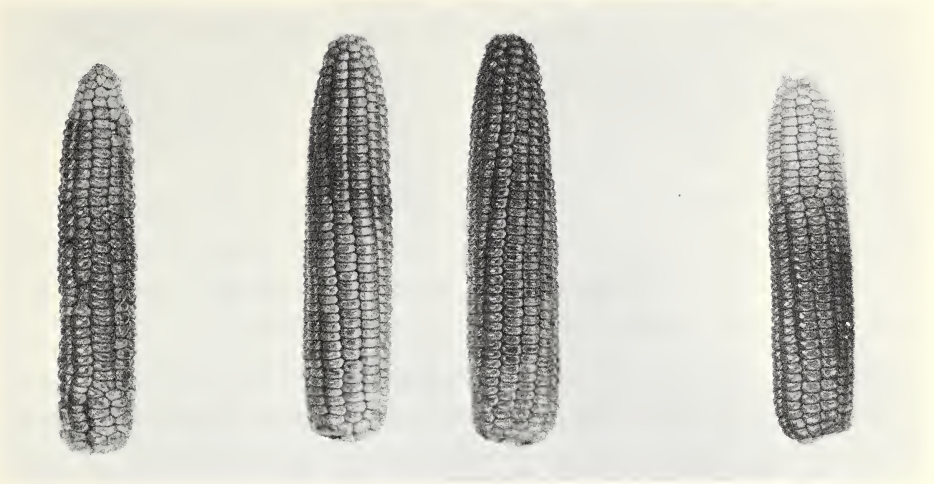


Figure 17 At the left representative ear of the inbred line called Purdue 51, at the right representative ear of the inbred called Purdue Bantam. The two ears in the center are representative of the single cross, called Golden Cross Bantam. This perhaps has been the most widely grown single cross of sweet corn both for freezing and canning as well as in home gardens. (Courtesy, Dr. Glenn Smith, U.S.D.A. and Purdue University)

tion is rather expensive, as inbred lines usually are low in yielding ability. Such single crosses (Smith, 1933) are grown extensively by the producer of sweet corn for canning and freezing, where uniformity of maturity and quality are characters of first importance.

2. The three-way cross. In this case a single cross is used as the female parent, which leads to excellent seed production in the crossing, or seed plot. This may be illustrated by the combinations, (A x B)C, (B x C)A, etc. An inbred must be selected as the pollen parent that has ability to produce an abundance of pollen. The female parent should excel in the production of excellent quality seed of satisfactory size and shape to produce the desired grades most popular with the grower.

3. The double cross. In this case both parents are single crosses, and the double crosses consist of the following types, (A x B)(C x D), (A x C)(B x D), etc. This is the most common method used in the production of seed for the commercial grower of field corn.

4. The inbred-variety cross. Produced from the cross of an inbred with an open-pollinated variety. This type of cross

has been used rather extensively as a first test of a series of inbred lines to determine their rating for general combining ability. Undesirable combining lines may be discarded on the basis that they give low comparative yields in test crosses.

5. The synthetic variety. Produced by random crosses between selected parental lines followed by seed production under open-pollinated conditions in an isolated seed plot, or in the center of a large seed plot of the synthetic. With 100 per cent cross-pollination, with equal viability of different gametes, and without selective fertilization or other selection pressure, the advanced generations are maintained without great genetic change. As the plants are cross-pollinated, there is an opportunity for continual recombination of characters. Natural or artificial selection may modify the variety from generation to generation. Selection for desirable plants, without selection for any particular plant or ear type, maintains a good variety under a constant state of relatively good productivity.

Synthetic varieties may be produced by crosses of inbreds in all possible combinations, or by a series of crosses such as (A x B), (C x D) and the cross of the first crosses (A x B) x (C x D), etc. The plants grown from this first complete combination (A x B)(C x D) are called the first synthetic generation or Syn 1. Random pollination of Syn 1 produces Syn 2, etc. Syn 2 may be thought of as the first production of a new synthetic variety. Such varieties may be of value under conditions where the yield does not warrant the use of high cost seed such as that of double crosses. Such synthetics are of value because seed selection in the commercial field may be used, as with open-pollinated corn, to propagate the variety.

Single crosses have, on the average, a little higher yielding ability than three-way or double crosses. Thus, from any four inbred lines it is probable that one of the 6 possible single crosses will excel the others in average yielding ability. Likewise, the best three-way crosses will be at least slightly superior in yielding ability to the best double cross possible among the four inbreds, although one of the difficulties is that not all inbreds are satisfactory as pollen parents. And finally synthetic varieties, on the average, yield less than single, three-way, or double crosses.

Some of these facts may be illustrated by the performance

of single crosses, with the knowledge that the yield performance, as well as other characters, of single crosses can be used with great accuracy to predict the yield of three-way or double crosses.

For illustration we may suppose that the six single crosses have the following yielding ability as determined by extensive comparative trials, A x B, 53 bu.; A x C, 52; A x D, 51; B x C, 50; B x D, 49; C x D, 48.

The yield of the double cross (A x B)(Cx D) can be predicted with great accuracy as follows:

Single Cross	Yield Bu.
A x C	52
A x D	51
B x C	50
B x D	49
Average	50.5

Both of the other two possible double crosses, (A x C) (B x D) and (B x C)(A x D), also have a predicted yield of 50.5 bushels. This resulted from the assumption made of yields of the single crosses. In many actual cases one of the three predicted yields is superior to the other two.

The highest yielding three-way cross in this case would be (B x C)A which would have a predicted yield as follows:

Single Cross	Yield Bu.
A x B	53
A x C	52
Average	52.5

Using the same method, (C x D)B would have a predicted yield of only 48.5 bushels.

The highest yielding single cross was A x B with 53 bushels, the highest three-way (B x C)A or 52.5 bushels, while each of three possible double crosses had a predicted yield of 50.5 bushels.

Inbred lines usually yield much less than normal corn. Excellent inbreds may in some cases yield about half that of their hybrids. For illustrative purposes, therefore, we have assumed the yield of each inbred as 25 bushels. What might

be expected from a synthetic variety made by crossing the four inbreds in all possible combinations? The average yield of the F_1 crosses in this case was 50.5 bushels. If we subtract the average yield of inbreds, 25 bushels, from the average yield of the six hybrids we obtain 25.5 bushels, which may be considered the result of hybrid vigor, or heterosis.

The theoretical yield of a synthetic variety produced from these six inbreds, and based upon the hypothetical yields used previously, may be obtained from the following formula of Wright (1922) where n = number of inbreds.

$$\text{Average yield of synthetic} = \frac{n-1}{n}(\text{Av. yield of } F_1\text{'s} - \text{Av. yield of inbreds}) + \text{average yield of inbreds} = \frac{5}{6}(50.5 - 25) + 25 \text{ or } 45.38 \text{ bushels.}$$

Both actual and theoretical expectations lead to the conclusion that, on the average, the best synthetic varieties will yield less than the best hybrids, although properly selected synthetics may be higher in productivity than normal open-pollinated corn. Richey *et al.* (1934) compared ten advanced generation double crosses in F_2 with that in F_1. Average yields of grain in F_2 were 15.2 per cent less than the F_1, *i.e.* that of the actual ten double crosses. In the illustration, on the theoretic basis given, the yield of the hypothetic double crosses was 50.5 bushels and that of an advanced generation synthetic was calculated as 45.38 bushels. In this case the calculated yield of the F_2 was 10.1 per cent less than the F_1.

Kiesselbach (1930) and Neal (1935) compared advanced generation single crosses in F_2 and F_3 with the yield in F_1. Kiesselbach obtained 67 per cent as much grain in the advanced generations as in F_1, while Neal's Syn 2 and Syn 3 yielded 70.5 and 75.7 per cent, respectively, as much grain as the F_1. Kiesselbach (1960b) presented further data on the performance of advanced generation corn hybrids including stover and fodder yields as well as grain. Mean yields of fodder for the F_2 single crosses were 78 percent of the F_1 as 100 and for double crosses 87 per cent. These results are in good agreement with those calculated by Wright's (1922) formula. Kiesselbach writes, "Application of Wright's production formula for F_2 hybrid performance is restricted to populations in which all component lines are equally represented." He emphasized that in three-way crosses, such as (A x B)C, that all lines are not equally represented.

As given previously the theoretical yield of a synthetic variety produced by the combination of inbreds is dependent upon two main causes. The expected yield of the average of all possible single crosses between inbreds used to produce the synthetic can be determined from actual trials. A determination of the average yields of the inbreds also must be learned from yield trials under the same conditions as for the single crosses. The difference between the average of all single crosses and the average of their parents may be attributed to heterosis. The extent to which this increased yield may be utilized by a synthetic depends also on the number of inbreds used in producing the synthetic, *i.e.*, if n inbreds are used, n-1/n of the yield due to heterosis theoretically will be retained by the synthetic. This calculation has been illustrated previously.

Various studies of synthetics in yield trials have been made and there has been relatively good agreement between the results and calculated expectations. The results of experiments were summarized by Kiesselbach (1960).

Hayes and others (1944) presented a study where a group of twenty-two selected, diverse inbreds, were studied in all combinations. From this study eight inbreds were selected that combined well in all possible single crosses. These inbreds then were used to produce a Synthetic variety. It yielded about as well as Minhybrid 403, which at that time was a desirable double cross. However, it was somewhat later in maturity and therefore not considered equal to the double-cross Minhybrid 403. It was distinctly superior to available open-pollinated varieties, not only in yield but also in important agronomic characters.

Selecting the Inbreds

The generalized method may be described as selection in self-pollinated lines, using Jones' terminology. This consists of self-pollination, and selection in each generation within and among lines, much as carried out by East, Shull, and others. The first step usually is to decide what open-pollinated varieties will be used in the production of inbred lines. Most breeders have used better yielding adapted varieties and have continued self-pollination and selection for about five generations until the inbreds appear relatively uniform. During this process

undesirable inbreds are discarded freely in all generations of selfing and selection. A common practice has been to test general combining ability by crosses with an appropriate tester in the S_4 (fourth selfed) or later selfed generation. The better combining inbreds then are selected and tested for performance in single, three-way or double crosses. More recently there has been a tendency to practice early testing, *i. e.*, to determine general combining ability in S_0, S_1, or some other early generation of the individual lines. Many of the characters of inbreds, such as ability to withstand lodging, growth habit characteristics, resistance to diseases and to insect pests, are rather closely correlated with the performance of their hybrids.

Figure **18** At the left of the photograph a row of a single cross of inbreds that have been selected for ability to withstand lodging. At the right, a row of the Morris Station strain of Minnesota #13. This variety excels in yield but lacks ability to withstand lodging.

Dr. Iver J. Johnson, Research Director, Caladino Farm Seeds, Inc., Willows, California, stands between the two rows. For many years Dr. Johnson was associated with the writer in corn breeding investigations in Minnesota.

Figure 19 The tassel of corn bearing the pollen grains which contain the male sexual cells. When approaching maturity the anthers which are filled with pollen grains are extruded as illustrated in the photograph. The pollen grains are carried by the wind and alight on the hairs of the silks where germination takes place. Normally the corn plant is almost entirely cross-pollinated and therefore corn is rather highly heterozygous. (Courtesy H. Kendall Hayes, Jr., Hybrid Corn Division, Cargill, Inc.)

Use of Inbreds in Hybrids

While the importance of diversity of origin has been rather extensively discussed it may be of interest to repeat previous conclusions and give at least one new illustration.

In the nineteen thirties Minhybrid 301 was released and grown extensively in Minnesota. It results from the crossing of a single cross, (11 x 14), from two inbreds of Minnesota #13 with B164, from Wallace, the latter being used as the pollen parent. This same three-way cross was introduced by the Pioneer Hi-bred Company under a different designation.

A little later Minhybrid 403 was produced and released by the Minnesota Station. The female parent also was (11 x 14). For this double cross (A374 x A375) was used as the male parent.

Holbert's well known A line was introduced and tested in Southern Minnesota. Even though it had been selfed for about eight years, lines A374 and A375 which matured somewhat earlier under Minnesota conditions than the original introduction, were selected from it. A375 was isolated from the A line a few generations after A374 was selected. In rather extensive comparative trials A375 has usually shown slightly higher combining ability in crosses with other inbreds than A374. When crossed together (A374 x A375) have sufficient hybrid vigor to make a satisfactory pollen parent.

The following illustration adapted from Crabb's story emphasizes the viewpoint that it often is of great value to use inbreds in one single cross parent that have a very distinctly diverse genetic origin from those in the other parent.

Yield trials in Iowa in the early nineteen twenties have been referred to by several writers who have discussed hybrid corn. Although these trials were somewhat more standardized than trials in other states at that time they were not very different from those used in other states, except that they were used more extensively in Iowa as a basis for stimulating farmers to become interested and to take an active part in the trials. However, the basic idea of a survey of available germ plasm was not different than in other studies.

In the fall of 1915, for example, the writer spent several weeks with Dr. W. L. Slate in a survey and collection of seed of farmers' varieties of corn in Connecticut. The collected samples of varieties were tested for performance. The better va-

rieties were used by Jones as a source of diverse material for selection in selfed lines.

From yield trials in Iowa a variety called Krug, entered by George Krug, proved rather outstanding. This variety had been selected previously by saving for seed the heaviest, most solid ears without paying attention to ear type. It was not a show corn. A story by Wallace in Wallace's Farmer emphasized the importance in Iowa of increasing yield by more extensive plantings of this variety. This led Lester Pfister, an El Paso farmer from Central Illinois, to grow Krug seed corn for sale. He entered his seed in the Iowa corn yield trial and it excelled in Iowa under conditions similar to those on Pfister's farm. He also started selfing in 1925. From two thousand selfed lines only about a dozen finally were selected. Richey visited Pfister in 1932 and obtained several inbreds, and after test by Richey at Arlington, Virginia, one line, Pfister's 187, was increased and distributed rather widely to other corn breeders.

About this time Pfister produced double crosses, and one of these proved to be better than the Krug open-pollinated variety. At a meeting of Holbert and Pfister in 1933 they agreed to exchange inbreds. Holbert crossed each of two of his better single crosses (A x Hy) and (A x 90), respectively, with a single cross of Pfister, and entered these in the Illinois University trials of 1934 as Experimental Doubles, 360 and 366, respectively. Pfister grew them under the designation, Pfister's 360 and 366. The results from the yield trials were favorable. Pfister distributed 665 bushels of hybrid seed in 1934 and by 1937, as the new hybrids continued to prove their value, he sold 37,000 bushels of hybrid seed.

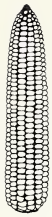
The remarkable performance led to great publicity for Pfister, and in the late thirties the Readers' Digest published an article on hybrid corn that gave the impression that Pfister was the sole discoverer and inventor of hybrid corn. The writer had not seen the article, but after it appeared he visited his barber in St. Anthony Park, St. Paul, who said, "Have you read about the remarkable discovery of Pfister? He has developed a new method of corn breeding that sounds almost like a miracle." I admitted I had not seen it but looked it up shortly afterward. Still another and new father of hybrid corn had appeared and from the article no one would have suspected that anyone else had ever taken part in hybrid corn development. This writer, however, wishes to pay his respects to Lester Pfister who, in spite of many difficulties, continued studies of inbreeding and

crossbreeding which led eventually, with the help of Holbert, to the production of excellent hybrids. It seems worth emphasizing, however, that the better hybrids, Illinois 360 and 366, or Pfister's 360 and 366, resulted from crosses of Holbert's best single crosses (A x Hy) and (A x 90) with the best single cross produced by Pfister.

These few illustrations could be supplemented with many others of a similar nature. They have been given here under the heading of, "Selection and use of inbreds in hybrids," to emphasize the fact that the final selection of inbreds is made on the basis of their use in specific hybrid combination where the most common method of use is the double cross.

After isolating the better inbreds and deciding how to use them in crosses, these are maintained by some method of controlled pollination such as previously described.

Chapter 13 BREEDING METHODS



Pedigree, Backcross, Convergent Improvement, Multiple Convergence

The Pedigree Method

There are various methods that can be utilized by the breeder in the production of improved inbreds. Each of these has certain advantages and disadvantages. Selection in selfed lines as usually carried out is a pedigree method where adapted open-pollinated parental varieties are the original source of germ plasm.

After the first cycle of breeding has been completed, the breeder may have a specific idea of the type of improvement needed and this may be accomplished by a controlled breeding program starting with crosses from known parents which together appear to have the characters desired.

In 1943 a program was started in Minnesota to breed corn for resistance to the European corn borer. During about six years the studies were carried out with the cooperation of research workers at the European Corn Borer Research Laboratory, Toledo, Ohio, Bureau of Entomology and Plant Quarantine, United States Department of Agriculture. Minnesota corn inbreds were tested at this laboratory, under manual infestation conditions in the field, for corn borer reaction. Since 1950 the work has been carried on in Minnesota in cooperation between the Departments of Agronomy and Plant Genetics and Entomology and Economic Zoology.

Each of the inbreds in three Minhybrids was crossed with an inbred from the Corn Belt that was thought to have tolerance to the European corn borer. Fortunately it was possible to use a different introduced inbred for each of the crosses. Each of these three Minhybrids was considered, at that time, the most

important Minhybrid for its zone of maturity, and the three hybrids were each adapted to a different maturity zone. The pedigree plan of procedure used in this study will be illustrated by describing the development of two corn borer resistant lines, A286, selected from the cross (A334 x Oh7) and A295, selected from the cross (A344 x L317).

Inbreds at the Minnesota Station are identified by the use of A. A334 was selected originally from Golden King, while A344 is U.S. 153, and was an introduced inbred. Both of these A inbreds have been used rather extensively, and A334 has been one of the parents in several Minhybrid varieties. Both A334 and A344 are borer susceptible.

The introduced inbreds used in the crosses, Oh7 and L317, are later in maturity than was considered desirable. In 1945, 4000 F_2 plants were grown of each of the two crosses (A334 x Oh7) and (A344 x L317). Desirable early maturing plants were selected, 77 plants being selfed from (A334 x Oh7) and 65 from the other cross.

In subsequent years, 1946 and 1947, each culture from a selfed ear was grown under manual infestation conditions at Toledo and rated for borer reaction. Cultures from the same selfed ears were grown at Waseca.

In 1948 the material from (A334 x Oh7) that remained in the trial originated from 16 F_3 lines while that from (A344 x L317) came from 27 F_3 lines. In this year single plant rows of 30 plants each were grown in the selfing plot, and two replications from seed of each selfed ear were grown for observation at the Waseca Station.

In 1947, when lines were in the F_4 or S_4 generation, selected lines had been grown also in an isolated crossing plot to produce seed for a test of general combining ability. This test was made in 1948. Inbreds A286 and A295 were resistant to first brood corn borers, were desirable as inbreds as learned from yield trials, and were classified as good combiners in these test crosses. The selected corn borer resistant lines, together with other desirable inbreds, were then used to make single crosses to predict the value of specific double crosses.

The final use of A286 and A295 has been in the double cross Minhybrid 414 (A286 x A295)(A73 x A375). The single cross used as the male parent had been used previously as a pollen parent. Inbred A73 was obtained from Wisconsin, and was selected there from a cross of G3 x A.R.9. A375, as explained previously, was selected at Waseca from Holbert's

Figure 20 At the left L317, an inbred highly resistant to attack of first brood corn borers. At the right, a plant of A344, highly susceptible to first brood borers. Grown under conditions of manual infestation of first brood borers. (From cooperative work of the Departments of Agronomy and Plant Genetics and of Entomology and Economic Zoology, Institute of Agriculture, University of Minnesota.

Figure **21** Two inbred lines maually infested with first brood corn borer larvae. The row at the left is a highly susceptible inbred, that at the right a highly resistant inbred. Taken at the time of maturity, Waseca Station. (Cooperative research, Agronomy and Plant Genetics, and Entomology and Economic Zoology)

well-known inbred line A.

Minhybrid 414 has been rather highly resistant to attacks of first brood corn borer and in this respect it follows the behavior of its two resistant inbreds, A286 and A295. In rather extensive yield trials Minhybrid 414 proved to be a high yielder. It is the result of what may be thought of as second cycle breeding for the inbreds used as the female parent of Minhybrid 414. Such second cycle breeding was carried out through a definite breeding plan, based on what seemed at the time to the breeder to be a desirable solution of the particular problem.

Backcrossing

In its most complete form backcrossing is designed to improve the recurrent parent by retaining most of its characteristics and adding some new character of definite value.

In self-pollinated plants backcrossing often is carried through six or seven generations. In corn breeding it has been used extensively to incorporate cytoplasmic male sterility and the restorer gene into inbreds for use in single, three-way, and double crosses.

Cytoplasmic male sterility, in the absence of dominant restorer genes, is inherited only through the female parent. Certain genetic factors modify its expression, and these must be eliminated, in some cases, by selection for completely sterile combinations. An inbred may be changed to carry sterile cytoplasm by backcrossing for sufficient generations using the cytoplasmic sterility parent as the female.

If it is desired to change A286 to a carrier of sterile cytoplasm, the breeder obtains a carrier of sterile cytoplasm, which may be designated as Ms, and carries out the following procedures.

1. Make the cross (Ms x A286), using Ms as the female.
2. Grow (Ms x A286) and pollinate with A286.

If the progeny are male sterile, the procedure may be continued for six backcross generations.

3. After six generations the resultant progeny should resemble A286 in all characters except male sterility.
4. The sterile form of A286, designated A286Ms, may be maintained by crossing it with A286 as a male.

Cytoplasmic male sterility in corn is complete if the material carrying a desirable source of cytoplasmic sterility, or

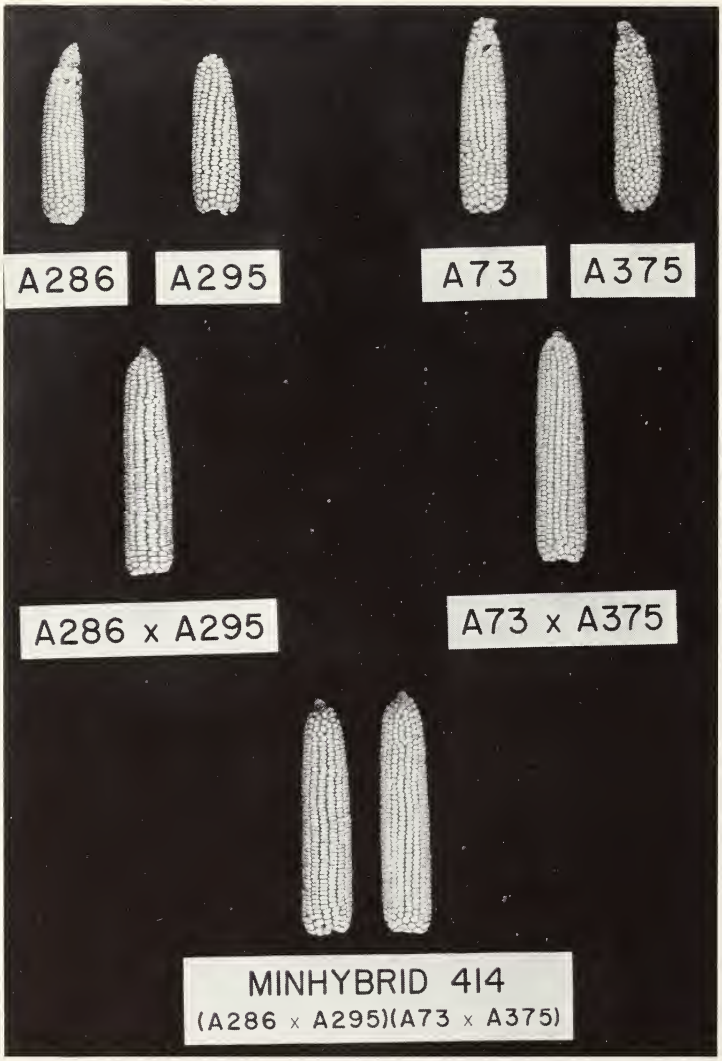


Figure 22

Illustrating the pedigree of Minhybrid 414. The inbreds A286 and A295 were selected from different single crosses of inbred lines, one inbred parent of each being resistant to first brood corn borer infestation.

The single cross (A73 x A375) is used as a desirable male parent in several Minhybrids, and both A286 and A295 give excellent single cross yields with both A73 and A375. The double cross is resistant to first brood corn borer attack. (Courtesy Minnesota Agricultural Experiment Station)

Ms, does not also carry partial, or complete restorer genes, or modifiers.

If A286 carried the *R*, or restorer factor, in a homozygous condition, it might be desirable to breed a line of A286 that lacked the restorer gene. In most cases inbreds when tested lacked the major restorer gene, and if modifiers are present, it has proven desirable to select plants for backcrossing that are completely sterile.

To illustrate use in a double cross, it will be accepted that A286 has been made into a cytoplasmic male sterile line, that it will be used in Minhybrid 414 (A286Ms x A295)(A73 x A375), and that A295, A73, and A375 lack fertility restorer genes.

The single cross (A286Ms x A295) can be produced by planting A286Ms and A295 in alternate row plots and saving seed from plants of A286Ms. The resultant single cross (A286Ms x A295) will be used as the female parent to produce double-cross seed of the type (A286Ms xA295)(A73 x A375). Seed from this double cross is blended with seed of (A286 x A295)(A73 x A375) to produce, when grown, sufficient pollen for the production of grain in the farmer's field.

To overcome the necessity of blending, restorer genes are bred into at least one of the inbreds of the single cross used as the male parent of the double cross. Thus, for Minhybrid 414 it will be necessary to add the restorer gene to either A73 or A375. If A73 is selected, it is then crossed with a known carrier, which may be called C, of restorer genes, and the following procedures carried out.

1. (A73 x C) when grown will be heterozygous, *Rr*. Backcross these plants to A73. About half of the progeny of this backcross will be *Rr* and half *rr*.
2. Grow the first backcross, select several plants and tag these as 1, 2, 3, etc. Use pollen separately from each to pollinate A73, and tag these A73 x 1, A73 x 2, etc. Cross a line carrying sterile cytoplasm as the female, called Ms, with pollen from 1, 2, 3, etc., and tag these Ms x 1, Ms x 2, Ms x 3.
3. Grow A73 x 1, A73 x 2, etc. also Ms x 1, Ms x 2, etc. If any line, such as Ms x 1 for example, shows about half of its plants to produce fertile pollen, then the seed of plants of the backcross designated as A73 x 1, will be used for the next backcross.

Figure 23

Illustrating a fertile and a male sterile tassel. This is a result of cytoplasmic sterility transmitted only by the female parent. In the absence of restorer genes, or factors for fertility, the progeny of satisfactory cytoplasmic male sterility plants are all male sterile. Restorer genes, however, are available that convert the progeny of cytoplasmic male sterility plants so that complete fertility is obtained in the progeny of crosses.

Cytoplasmic sterile lines may be maintained by crossing with male fertile plants that have been bred to be of the same genotype, i.e. , have the same genetic factors, as the inbred cytoplasmic sterile parent but that carry normal cytoplasm.

4. Continue backcrossing as outlined under 3 until six backcross generations are completed.
5. Selected plants from this last backcross may be selfed and about one out of four plants of progenies carrying the restorer gene will be homozygous. Each selected plant can be tested by crossing with a line carrying the Ms cytoplasm.

In all combinations the results are not always as simple as has been outlined. Therefore, before cytoplasmic male sterility lines are accepted for use their ability to transmit complete male sterility in the cross to be made is tested by growing and studying the crosses. Complete male sterility of all plants of the progenies studied is essential. Similarly the converted lines carrying the restorer factor are tested in the crosses where the restorer gene is needed to be sure that they satisfactorily restore fertility.

In a similar manner backcrossing may be used to change

a known double cross to the waxy endosperm condition by changing the normal factor for starchy endosperm *W* in each of the four inbreds to the recessive homozygous condition symbolized by *ww*. This has actually been done.

These illustrations of modifying lines by backcrossing seem excellent examples of backcrossing technics designed to modify known inbreds by changing a specific character.

Convergent Improvement

In some cases of backcrossing it may not be necessary, or desirable, to make as many backcrosses. That is the situation in using backcrossing as a technic in convergent improvement.

The convergent improvement technic first suggested by Richey (1927) has been discussed already as a method of testing the hypothesis of dominance of linked growth factors as one cause of heterosis. His philosophy was about as follows. If one selects a good single cross as (A x B), and accepts the idea that the vigor of the F_1 is the result of partial or complete dominance of growth factors, then by double backcrossing new inbreds may be obtained where A is improved by characters from B, and B by characters from A. When these recovered inbreds are crossed, and with a lack of perfect dominance in some crosses of A_B, *i.e.*, A with some characters of B, with improved B_A, the resultant hybrid should be superior to original A x B. The recovered lines A_B and B_A should be more desirable as inbreds than the original selfed lines, A and B.

In studies of this and similar problems it was learned that in selecting for vigor of plant growth during the process of backcrossing, two and at the most three generations of backcrossing were all that could be used if the breeder were to have very much chance of improving vigor and greatly modifying the inbreds. Recovered inbreds would need to be selfed for as many subsequent years as necessary, as backcrossing theoretically leads to homozygosis as rapidly as selfing. If only two or three backcrosses are made before selfing, then it is necessary to produce enough inbreds to find combinations of $(A_B \times B_A)$ as desirable as (A x B), or more so, in the production of hybrid vigor.

Extensive studies of convergent improvement have been made by Richey and Sprague (1931b), Murphy (1942), and Hayes *et al.* (1946b). It does not seem feasible to present results of

these studies in great detail. Murphy studied recovered lines from the two single crosses (C15 x C19) and (C16 x C20). After two, three, or four years of double backcrossing, the lines were selected and selfed for two years. Test crosses were made of the type (recovered C15 x C19), (recovered C19 x C15), etc., for each single cross group. Fifty-one such crosses were compared with the respective original single crosses in yield trials. The results were placed in yield classes of 0, +1, +2, etc., of the calculated standard error of a difference, where the 0 class represented the yield of the respective original cross (C15 x C19), or (C16 x C20). Eleven crosses, between recovered lines and the original non-recurrent parent, were placed in classes of -2 to -5 lower yield than the checks, and only one cross was in the +2 class. Seventeen test crosses were made between recovered lines that were among the more desirable from the first test and again compared with the original crosses in yield trials. Of these seventeen, two were placed in the +2 class, and two in the +4 class. Under the conditions of the experiment the two crosses in the +4 class appear to be distinctly higher in yield than the original cross.

The studies reported by Hayes and others were started at the Waseca Station by Doxtator to determine the value of convergent improvement for Minhybrid 403 (11 x 14)(A374 x C23).[1] The inbreds of Minnesota #13, 11 and 14 are much earlier in maturity than A374 and C23. A374 was selected at Waseca directly from Holbert's A line, and C23, also from Holbert, was later in maturity than Holbert's A. The original single crosses for this study then were (11 x C23) and (14 x A374).

The studies of backcrossing and selection carried out for the Waseca convergent improvement program were handled in about the same manner as the studies reported by Murphy, except that all phases of the work were more extensive.

Double crosses from recovered lines were compared with Minhybrid 403 in extensive yield trials, and several of these yielded significantly more than 403. None was as desirable, in its maturity class, as the better double crosses from other breeding programs.

[1]Before introducing Minhybrid 403, the inbred A375 isolated from A374 was substituted in the pedigree, in the place of C23, as this combination gave equally as good yield as the original Minhbrid 403 and was earlier in maturity. This explanation is made to show why convergently improved Minhybrid 403 was compared with 403.

The results of these studies are in agreement with the hypothesis of partial dominance of linked factors as an explanation of heterosis. The progress of improving an inbred by convergent improvement was substantial for 11 and 14 and much less marked for C23 and A374. This leads to the conclusion that by convergent improvement, or backcrossing it is possible to retain the character of specific combining ability of an inbred, and in some cases at least to greatly improve the inbred itself, especially if the inbred has clear-cut weaknesses.

Lonnquist (1960) studied convergent improvement of (Wf9 x 38-11). This single cross, that has been used rather widely in double crosses in the Corn Belt, was selected primarily to improve the pollen shedding ability of Wf9, and also because the single cross Wf9 x 38-11 gave excellent heterosis. Usual methods were used in the convergent improvement program except that recovered lines were tested also in top crosses.

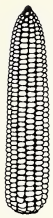
Recovered lines that yielded well in top crosses were then used in 5 double crosses. The yields of the 5 double crosses, from recovered lines as one parent, were compared with double crosses where the original single cross Wf9 x 38-11 was used as a parent. In all 5 comparisons the double crosses made from recovered Wf9 x recovered 38-11, yielded more than comparable double crosses where the original single cross Wf9 x 38-11 was one parent. However, the double crosses where recovered Wf9 x recovered 38-11 was a parent, were also somewhat higher, on the average, in moisture content.

Lonnquist discussed the convergent improvement studies of Hayes *et al.* previously reviewed where convergent improvement was carried out by using inbreds of one of the single cross parents with inbreds of the other single cross parent. He writes, "In spite of this, the authors were able to obtain improvement in the resultant hybrids compared with the original hybrid." He apparently overlooked the fact that Hayes *et al.* used a method that gave opportunity for greater improvement in the inbreds themselves. This was accomplished.

Multiple Convergence

Richey (1946) suggested a plan of breeding called multiple convergence and gave a limited amount of data regarding its value. The idea consists of improving and modifying an inbred by convergence of diverse small sources of germ plasm as trib-

utaries to one larger source. If A is a very desirable inbred in crosses it was suggested that A be modified by two separate backcross programs from sources C and D, with the eventual idea that $A_C \times A_D$ might be sufficiently vigorous to use as a male parent of a double cross. It seems probable also that recovered lines could be obtained that were equal or superior to A in specific crosses where A previously was known to be a desirable parent. The viewpoint here is that recovered A_C or A_D lines might be improved by adding desirable genes from C and D, respectively, and therefore selections of A_C or A_D might be used instead of A, in crosses where A previously had proven desirable. This could be determined only by actual test.

Chapter 14  BREEDING METHODS

Principles of, Early Testing for Combining Ability, Recurrent Selection, Gamete Selection, Reciprocal Recurrent Selection

Early testing for combining ability in corn consists of the following steps. At the time of selfing the S_1 or S_0 plants, they are outcrossed to a tester to measure yielding ability and general performance. After the tests the individual plants or lines selected for further use consist of those that excelled in combining ability. These are used for growing progenies for continuation of inbreeding where visual selection in selfed lines was practiced, or they are used for making crosses among superior lines, and combining seed of these crosses as the first step in recurrent selection. The tests for general combining ability are made by crossing all lines to an open-pollinated variety to make inbred-variety crosses, or to some other tester or testers that represent variable genotypic complexes. If a test of specific combining ability is needed the test crosses are made with specific testers, such as an inbred or single cross parent selected from appropriate sources.

Early testing for general combining ability was proposed first by Jenkins (1935) who concluded from a study of S_1 and comparable later generations of selfing that, "The inbred lines, particularly the Iodent lines, acquired their individuality as parents of top-crosses very early in the inbreeding process and remained relatively stable thereafter." All of the information from numberous experiments, many of which were reviewed by Hayes *et al.* (1955), lead to the conclusion that there are marked differences in the combining ability of the inbred lines isolated from S_0 or S_1 lines by continued selfing or selecting, whether the lines were classified in tests as high, medium, or low combiners.

The studies indicate also that the lines descending from S_0 or S_1 plants of high combining ability, as determined from test crosses, are superior in combining ability, on the average, to lines from S_0 or S_1 plants that in test crosses were classified as medium or low combiners. This naturally should be the result as there are several experiments demonstrating that combining ability is inherited in about the same manner as other quantitative characters. It also is very evident that lines that prove to be high or low combiners in test crosses made in S_0 and S_1 material, are not necessarily homozygous for this condition, but may, in many cases, segregate for combining ability during the process of selfing.

The problem of early testing also has a definite relation to the effects of visual selection, during inbreeding, upon combining ability. Osler *et al.* (1958) refer to an earlier study in Mexico of the Rockefeller Foundation Program in which it was concluded that visual selection, in locally adapted varieties during selfing, was of little or no practical value in modifying combining ability in specific combinations. Jones and Mangelsdorf (1925) concluded that, "effective selection must be based upon performance of the plants after homozygosity has been reached." This conclusion, however, was reached before extensive studies of early testing had been made.

The more recent studies of Osler and others include comparisons of single crosses between S_1 lines with the same number of single crosses from advanced generation lines of the same origin, produced by visual selection during the selfed generations. There were forty-five comparisons of S_1 x S_1 and S_4 x S_4 in 1951, and ninety-one similar comparisons in 1952 and 1955 inclusive, where S_1 x S_1 combinations were compared with S_A x S_A crosses, S_A indicating lines that had been inbred with visual selection during subsequent generations after S_1. In the studies of Osler and others the number of selfed generations of S_A lines was not always given. The S_1 lines used apparently were only the more desirable ones.

The inbreds used in the study were of two sources, local and introduced. Local lines were derived from varieties collected in the Valley of Mexico in the vicinity of the Chapingo Experiment Station. The introduced lines were selected from varieties collected in surrounding states but from areas of similar altitude to that of Chapingo.

In 1952 and 1955 the comparison of each S_1 x S_1 cross with S_A x S_A, was made by the use of the "t" test for differences be-

tween paired plots. In 1951 the "t" test was also used but the plots were not paired.

Table 20 summarized the comparisons for three types of crosses.

Table 20 Summary of Yield Differences of S_1 x S_1 Crosses Versus Crosses Between their Derived Advanced Lines

Kind of Cross	Number	Crosses better as		Crosses not significantly different
		Advanced	S_1 lines	
Local x local	20	8	4	8
Local x introduced	77	44	14	19
Introduced x introduced	37	24	6	7
All crosses in percentage		57	18	25

Average yields in bushels per acre of single crosses involving S_1 lines (S_1 x S_1) and of the single crosses made from the more advanced lines of the same origin, (S_A x S_A), are summarized in Table 21. The averages are of all crosses including those in which S_A x S_A was superior, those in which S_1 x S_1 yielded significantly more than S_A x S_A, and those in which the difference was not significant. (See Table 21)

Table 21 Average Yield of S_1 Crosses and Comparable Advanced Generation Crosses in Bushels per Acre

Kind of Cross	Number of Comparable Crosses	Average Yield in Bushels per Acre		Average Difference
		S_A x S_A	S_1 x S_1	
Local x local	20	73.2	68.8	4.4
Local x introduced	77	76.5	69.7	6.8
Introduced x introduced	37	71.0	62.0	9.0

In each case the average superiority of S_A x S_A over S_1 x S_1 was of considerable significance and importance. If one accepts the viewpoint that with random selection during selfing S_1 x S_1 crosses may be expected to yield as well as S_A x S_A crosses, on the average, then the differences may be ascribed to visual selection during selfing.

The improvement in yield and ear appearance was greater

in crosses between introduced than from local lines, and that for plant appearance was greater in crosses of local lines than introduced. Crosses between Local x Introduced yielded better, on the average, than either Local x Local or Introduced x Introduced. These results are in contrast with those of Sprague and Miller (1952) who concluded from statistical tests of data on combining ability that visual selection during inbreeding was ineffective as a means of improving combining ability.

When all of the evidence is considered it seems reasonable to the writer to conclude that, on the average, visual selection during inbreeding may be expected in the majority of cases to lead to an improvement in general combining ability of the resultant lines.

Recurrent Selection

Sprague and Brimhall (1950) credit Hayes and Garber (1919) and East and Jones (1920) with first using recurrent selection to develop inbreds and corn synthetics with higher protein content.

The Minnesota study (Hayes, 1922) which was a continuation of that reported by Hayes and Garber may be used for illustration. Selection in selfed lines of Minnesota #13 resulted in the isolation of two high protein inbreds. These were crossed, the F_1 and F_2 were selfed, and F_3 progenies were grown from seed of F_2 plants. The F_1 in this case yielded about 10 per cent more than Minnesota #13 and was about two per cent higher in protein content. Reciprocal crosses were made between F_3 plants, and the protein content of the resultant ears was analyzed. Seed was composited of crosses made between plants where the ears of both parents were high in protein content. Plants from this bulked seed were grown in an isolated plot under conditions of normal open-pollination. Yields were determined in grams of grain per plant from this plot in comparison with yields in a similar plot of Minnesota #13. While the comparison is not very reliable the results appear of some interest. (See Table 22)

This is an illustration of recurrent selection. Reciprocal crosses of F_3 plants were analyzed for protein content, and selection of crossed ears in F_3 for producing the synthetic was made on the basis that both parents produced ears of high protein content.

Table 22 Comparison of Protein Content of Minnesota #13 and a Synthetic Produced by Recurrent Selection

Origin	Grain Yield per Plant	Protein Content
	Grams	Per Cent
Minnesota #13	122.6	12.01
Synthetic	122.6	14.99

Because of the interest in, and importance of recurrent selection, it seems desirable to summarize Jenkins' (1940) suggestions for breeding synthetic varieties by using inbreds from early generations of selfing that have high general combining ability as determined by early testing. This seems to be the first outline of the procedures used in recurrent selection, although Jenkins did not use this terminology.

Jenkins suggested these methods as a means of improving an open-pollinated corn variety for use in conditions where the use of hybrid seed was not feasible. The essential steps are:

1. The production of S_1 selfed lines.
2. The testing of these lines for general combining ability in inbred-variety crosses.
3. Intercrossing the lines that performed the best in inbred-variety yield trials.
4. Growing the synthetic under isolation for one or more generations.
5. Repeating the procedures as outlined under 1 to 4, inclusive.
6. Adding inbreds from other sources to the synthetic, when, and if, that appeared desirable.

Hull (1945) gave a detailed description of recurrent selection, particularly in relation to specific combining ability with an inbred. He writes (1952), "Recurrent selection was meant to include reselection generation after generation, with interbreeding of selects to provide for genetic recombination," also, "Thus selection among isolates, inbred lines or clones, is not recurrent until selects are interbred and a new cycle of selection is initiated."

Since the breeder of corn desires to isolate inbreds of either high general or high specific combining ability, or both, recurrent selection in corn breeding usually involves early test-

ing for combining ability before the selects are interbred.

In a general program for producing inbred lines of high general combining ability the steps to be carried out may be illustrated as follows:

1. Selection of material to use in the study. This might consist of an outstanding open-pollinated variety such as Krug, a synthetic variety produced by combining desirable inbred material, seed of desirable double crosses or some other suitable population that is genetically variable. It seems worth emphasizing the desirability of maintaining at least two separate populations or synthetics, where so far as possible the two sources were of diverse origin. Essential procedures for each separate origin are given under 2 to 6.
2. Selection of S_0 or S_1 plants that are self-pollinated and each crossed to a tester.
3. Yield trials of test crosses and the selection of the better ten combining lines.
4. Intercrossing these, using remnant S_0 or S_1 seed, to produce a synthetic.
5. Repeat 2 to 4 for as many cycles as is desired.
6. Inbreeding through 4 or 5 selfed generations after any desired cycle of recurrent selection and the use of the resulting inbreds in hybrids.
7. If two sources of diverse origin have been recurrently selected in separate programs, double crosses will be produced of the type of cross, (A x A)(B x B), where inbreds from one source are designated as A and those from the other as B.

In many cases recurrent selection may be used for specific combining ability. If one has a double cross (A x B)(C x D), it is possible to determine the relative value in the hybrid of each of the inbreds. To compare the combining ability of the inbreds, A and B, one may compare the crosses (A x C) + (A x D) with those of (B x C) + (B x D) or A(C x D) may be compared with B(C x D). In the same manner the specific combining ability of C and D with (A x B) may be determined. To illustrate hypothetical yields are taken.

In this case the specific combining ability of A with C and D was 70 bushels, while that of B with C and D was 80 bushels. It seems apparent that the yield of (A x B)(C x D) could be increased by five bushels per acre if A was improved in specific

combining ability so that it was equal to B. It seems evident that the testers used will be dependent upon the type of program under study.

Combining Ability of A		Combining Ability of B	
Cross	Yield bu.	Cross	Yield bu.
A x C	68	B x C	78
A x D	72	B x D	82
Average	70	Average	80

Gamete Selection

Stadler (1944) suggested a method which he called gamete selection particularly for further selection of material from open-pollinated varieties. His idea was that a good gamete from a random population of a variety occurred much more frequently than an equally desirable zygote. Thus in a variety, or other comparable source, if a reproductive cell with high combining ability occurred once in 100, an equally desirable plant produced from fusion of two such high combining gametes would occur only once in 10,000 plants. He thought it would be much easier, therefore, to use gamete selection as a method of obtaining inbreds for improving specific crosses than to attempt to isolate new inbred lines by the usual technic of selection in selfed lines.

The method may be illustrated in its relation to the improvement of inbred A in the double cross (A x B)(C x D) where A gave 10 bushels lower yield than B in crosses with (C x D). The source of gametes in this case may be an adapted variety, V, not yet extensively used as a source of inbreds.

The following procedures would be used:

1. Pollinate A with mixed pollen from desirable plants of V, selected as a source of gametes.
2. Self selected plants from these crosses, and use pollen of each individually to pollinate plants of C x D.
3. Test these crosses produced by step 2 in yield trials, studying all characters of importance, including yield, in comparison with crosses of A(C x D).

Two methods could be followed subsequently, depending on the plan selected.

Method 1. This might be considered only as an early testing program used in gamete selection. At the end of the first cycle of early testing, selection in selfed lines may be carried out from the original selfed plants from step 2, that in the test in crosses with C x D proved to be the more desirable combinations.

Method 2. If recurrent selection appeared desirable about ten of the better performing crosses could be selected, and seed of the original selfed plants used to produce a synthetic. After a generation of propagation to insure recombination of genetic factors a second cycle of breeding could be initiated. Selected plants from this population could be handled as in step 2 and step 3 as outlined.

After two or more cycles of recurrent selection had been completed selection in self-pollinated lines maybe made to isolate new inbreds to take the place of A in the double cross (A x B)(C x D). There is no reason to conclude *a priori* that an inbred may not be obtained that combines with (C x D) even better than B does.

Reciprocal Recurrent Selection

To complete a discussion of recurrent selection, the method of reciprocal recurrent selection as outlined by Comstock *et al.* (1949) will be briefly outlined. These writers suggested the use of foundation material from two sources that are genetically diverse and which combine well together to give a desirable hybrid. The sources for ease of presentation may be referred to as A and B, and the material from these sources probably should each be heterozygous. If homozygous, the method of work would be somewhat analogous to convergent improvement.

The methods proposed by Comstock *et al.* were designed primarily to test the probable importance of various types of factor action and interaction as an explanation of heterosis. In the presentation of the method the procedure given here has been modified in certain respects from that outlined originally by Comstock and others.

Individual plants of sources A and B are selfed, and pollen from each of the selfed plants of A is used to pollinate plants of B. Thus B is used as a tester to select plants of A that combine more satisfactorily with B. In this series recurrent selection of A source material is continued by intercrossing proge-

nies, for example, ten selected S_1 lines of A in all combinations, to produce a synthetic. In its most desirable form this synthetic may be increased until Syn 2 is produced.

In a similar manner Syn 2 of the B source would be obtained.

In the second cycle of recurrent selection the individual selected plants of Synthetic A would be tested for combining ability with Synthetic B, and individual selected plants of B would be tested for combining ability with Synthetic A. The completion of the second cycle of breeding would then be carried out in the same manner as in the first cycle.

After completion of as many cycles as desired, or at the end of each cycle if that seemed worthwhile, selection in selfed lines could be practiced, with the intention eventaully of producing double crosses of the type (A x A)(B x B) where the inbreds A were obtained by the method of selection followed from the A source and the B selected inbreds from the B source.

Cyclic selection could be followed as long as there was definite increased variability in a positive direction.

Chapter 15 BREEDING METHODS

Introduction, Some Results of Gamete Selection, Early Testing and Recurrent Selection, Early Testing and Recurrent Selection in Producing Synthetics

The value of recurrent selection is dependent to a considerable extent on the genetic variability of the material worked with, the extent to which this variability in the positive direction continues to be expressed during various cycles of recurrent selection, and the degree of heritability of the character under study, which is basic to a determination of the degree of accuracy which the breeder can attain in selection of the more desirable genotypes.

For some characters such as oil content the reaction of individual plants can be used with a great deal of accuracy in selection for high oil content as demonstrated by Sprague and Brimhall (1950). Likewise for disease and insect resistances, under conditions of infection with individual pathogens or insect pests, individual plant selection of resistant plants can be used efficiently, as was demonstrated by Jenkins *et al.* (1954), for resistance to leaf blight caused by *Helminthosporium turcicum*. For certain characters such as yielding ability and ability to withstand lodging, however, the technic of early testing has proven of value as a means of efficient selection of genotypes that have the desired character. Thus early testing in itself is not a method of breeding but a technic of evaluation that makes possible an early evaluation of the performance of selections in test crosses. However early testing for many characters is an essential step in both gamete selection and in recurrent selection.

This chapter will be confined largely to a review of experimental results which demonstrate the ways in which gamete

selection and recurrent selection may be used and the effectiveness of them.

Gamete Selection

Gamete selection as presented by Stadler (1944) may be illustrated by the study of Pinnell *et al.* (1952). This part of the study was carried out to obtain an inbred to replace A25 in the double cross (A25 x A334)(A73 x A375). In this cross A25 was somewhat lower in combining ability than A334 in crosses with A73 x A375, as determined from the averages of single crosses (See Table 23).

Table **23** Relative Yielding Ability of A25 and A334 in Crosses with A73 and A375

Crosses Compared	Average of Crosses	
	Per Cent Moisture	Bushels
A25 x A73, A375	24.6	76.2
A334 x A73, A375	24.7	79.4

The yields given are on a comparable moisture basis of 15.5 per cent, and the percentage moisture given was that of the grain at harvesting time.

The Golden King variety had proved to be an excellent yielder in extensive trials and a relatively desirable open-pollinated variety. It is of some interest that A334, which has been used extensively in Minnesota double crosses, was obtained from Golden King by selection in self-pollinated lines.

Approximately 60 F_1 plants of A25 x Golden King were selfed and crossed with (A73 x A375). On the basis of appearance of the selfed plants at harvest, 32 crosses with (A73 x A375) were selected to test in yield trials. Of these, the yields of ten were in the class of +1 of the calculated L.S.D. at the 5 per cent point, where the yield of A25(A73 x A375) was taken as the standard or 0. There were twenty-two test crosses with average yields in classes of -1 and -2. Therefore no progenies tested were significantly higher in yield, although eight of the ten were lower in moisture percentage than the test cross A25(A73 x A375).

As a result of many years of study under Minnesota conditions it has been concluded that there is, in general, a positive relation between yield and moisture content at husking. To place material on a comparable basis both moisture percentage at husking and yield have been considered together by the calculation of a performance index using the cross of A25(A73 x A375) as 100 for both moisture at husking and yield. If, for example, a plant of Golden King x A25 in a test cross gave a moisture percentage of 93.5, as compared with A25 x tester, and a yield of 106.5 per cent, its calculated performance index would be +13.

Six of the thirty-two selfed plants of the F_1 of Golden King x A25 were selected; three plants which had a high performance index in test crosses, and three of low performance, as compared with A25(A73 x A375). Selfed progenies of these plants were grown in F_2, individual plants were selected, selfed, and crossed with (A73 x A375). These crosses were grown in yield trials and the results placed on a performance index basis. The results are summarized in Table 24.

Table 24 Frequency Distribution of Performance Indices of F_2 Progeny Plants from (A25 x Golden King) x Tester Around Mean Performance of A25 x Tester

F_1 Plant Number	Indices for F_2 Plants					
	-15	-5	+5	+15	+25	+35
19 H*				1	2	2
20 H			2	3	2	
36 H			3	4		
5 L		3	2	1	1	
29 L		1				
46 L	1	1	5			

* H = high performance index; L = low.

There is a marked difference, on the average, between the performance of individual plants selected from the high lines and those from the low lines and, even with this small sample, rather wide differences between plants within lines.

It is interesting to compare the tests in F_1 with those in F_2 for these six selected lines (See Table 25).

Table 25 Performance Indices of Test Crosses of Selected Plants of F_1 and F_2 Progenies from A25 x Golden King, where the Tester was A73 x A375

F_1 Plant	Performance Index			Number of F_2 Plants
	1947	1949		
	F_1	F_1	F_2	
19 H	+11	+19	+25	5
20 H	+14	+ 9	+14	7
36 H	+ 9	+16	+11	7
5 L	-11	- 3	+ 5	7
29 L	-11	- 1	- 0	1
46 L	- 5	+ 1	+ 2	7

There was a relatively good relationship for the performance of the F_1 test crosses in 1947 and 1949. Visual selection of F_2 plants appeared to have been of value, as means of test crosses of the F_2's exceed those of the F_1's on an average.

The statement by Pinnell *et al.* (1952) seems of interest. They wrote, "Whether selection of gametes should be followed by test controlled selection in the F_2 is an important question. In these studies more than 50 per cent of the F_2 plants from high combining gametes tested at least ten performance index units higher than the sampler inbred. Thus without further test crosses, the chances of choosing high combining F_2 plants would still have been very good. It was very evident from field observations that the proportion of agronomically desirable F_3 lines appeared lower than usually found from crosses of highly selected inbreds."

This would seem to indicate that after one cycle of gamete selection, where gametes from open-pollinated varieties are used, it would be desirable to grow larger numbers of progenies and practice visual selection by the pedigree method.

Lonnquist and McGill (1954) made an interesting study of gamete selection with the three-way cross Nebraska 501,

Table 26 Yield Performance in 1947 of Six Selected Crosses of Hays Golden x N6, Representing a Seriated Sample; and in 1949 of the crosses with (Wf9 x Hy) of about 20 Selected Plants of Each of the Six Progenies, Compared with Yields of Crosses of Three Well Known Inbreds with (Wf9 x Hy), Where the Yield of (Wf9 x Hy)N6 is Taken as Class 0.

Plant Source of Gametes	Yield H.G. S_0 Plant x N6 1947	Class Centers in +1 to -7 to -10 Standard Errors of a Difference about the Mean of (Wf9 x Hy)N6 as Class 0					Gametes Tested	Mean Yield
	Bushels	-7 to -10	-4 to -6	-1 to -3	0	+1	No.	Bu.
HG 96	52.6		2	9	10	1	22	95.8
HG 3	46.6	1		10	9	1	21	94.9
HG 21	45.3		2	16	1	1	20	92.9
HG 5	43.8	2	3	16			21	89.4
HG 14	32.7	1	8	11			20	88.4
HG 76	25.3		12	7			19	86.6
N6					1			98.9
R4				1				91.0
M14				1				89.0
L317			1					86.6

(Wf9 x Hy)N6, which is one of the higher performing hybrids in several areas in Nebraska. The purpose of the study was to develop another inbred line which could be used in a double cross to replace the three-way. The source of gametes was Hays Golden yellow.

Initial crosses were made in 1946 in an isolated plot using Hays Golden as the female and inbred N6 as the male. Several thousand plants of Hays Golden were grown, and 118 desirable plants were selected and top-crossed for yield testing. The yield test was made in 1947, and from the results six top-crosses were selected, representing a seriated sample, for further gamete sampling purposes. These six top-cross families were planted from remnant seed in 1948 and about 20 plants in each family were selfed and out-crossed to (Wf9 x Hy). These test crosses were grown in a triple lattice design with six replications in 1949. From this test the five best (N6 x HG) selfed plants in each of the six families were selected, and their progenies sampled and test crossed with (Wf9 x Hy). The yield trial was completed in 1952 with six replications.

The yield in 1947 of the six crosses selected as a seriated sample, and the yields of top-crosses with (Wf9 x Hy) of about 20 plants within each family are given in Table 26. These yields

are presented in terms of classes of +1 to -7 to -10 times the standard deviation where the yield of (Wf9 x Hy)N6, which was used as a standard was class 0. Yields of crosses of three well known inbreds with (Wf9 x Hy) are included also.

Of the 123 gametes tested about 18.7 per cent were equal or superior to N6 in test crosses with (Wf9 x Hy). These superior gametes were from three of the sources representing the upper half in yield of the seriated sample of Hays Golden S_0 plants x N6. In this trial the crosses of R4, M14, and L317 with (Wf9 x Hy) yielded less than crosses of the better plants of Hays Golden x N6 with (Wf9 x Hy).

From each of the six families of Hays Golden x N6, where about 20 plants in each family were tested in crosses with (Wf9 x Hy), the five best crosses were selected on the basis of their performance in comparison with N6(Wf9 x Hy) placed in class 0. The selfed plants used in these five best crosses in each of six families were again crossed with (Wf9 x Hy) to determine the value of the first selection. It is apparent from data in Table 27 that there was a relatively good relation between the mean yields in 1949 and the performance of the selected top-crossed plants.

Table 27 Mean Yield of Gametic Sample of Six Families of Hays Golden x N6 and Yield of F_1 Plants from the Six Families of Hays Golden x N6 When Crossed with (Wf9 x Hy), Compared with (Wf9 x Hy)N6

Parentage	Gametic Sample Mean 1949 Bu.	Class Centers of ±1, 2, 3, etc., times the Standard Error of a Difference about the Mean of (Wf9 x Hy)N6							Mean Bu.	Range of Individual Test Crosses Bu.
		-5	-4	-3	-2	-1	0	+1		
N6	98.9						1		135.8	136
HG 96 x N6	95.8						3	2	139.1	126 - 150
HG 3 x N6	94.9					1	3	1	135.2	119 - 150
HG 21 x N6	92.9				1	2	2		132.1	116 - 148
HG 5 x N6	89.6			2	2	1			126.2	115 - 136
HG 14 x N6	88.4			2	0	2	1		129.5	114 - 144
HG 76 x N6	86.6	1	1	0	3				122.8	95 - 140

There may be some difference of opinion regarding the type of top-cross used to select the original gametes from Hays Golden. This could only be determined by test comparisons. The writer would have preferred to have used top-crosses with (Wf9 x Hy) for this selection. The method used, however, appeared to give satisfactory results. It seems reasonable to con-

clude that selection in self-fertilized lines should isolate inbreds, which would be useful in producing the male single cross of a double cross with (Wf9 x Hy), either in combination with N6 or with one another. The double cross would have the pedigree (Wf9 x Hy)(selected inbred x N6) or (Wf9 x Hy)(selected inbred x selected inbred). In either case the second cycle breeding would result in improving certain inbreds of a well known hybrid, and in this way would produce an improved hybrid.

Some Results of Early Testing and Recurrent Selection

The method of early testing seems of particular value when the breeder wishes to obtain an improved inbred to use in a specific double cross. It may be of value also in those cases where inbreds are selected from a desirable source such as a stiff stalked synthetic, or a synthetic produced from inbreds that have resistances to special diseases or pests, for example a synthetic that was resistant to the first brood corn borer. The method presented by Jenkins, and previously summarized, consisted of early testing and recurrent selection for the production of an improved open-pollinated synthetic variety.

The long-time study in Illinois of selection for high and low oil content and high and low protein, has become of classical interest. The summary given here is similar to that in Hayes *et al.* (1955).

The original study was initiated in 1896, with foundation seed stock of 163 ears of the Burr White variety. Four selected strains have been established called High Oil, Low Oil, High Protein and Low Protein, respectively.

Although there have been modifications of technic throughout the study, these probably do not greatly affect the results.

For the first twenty-eight generations ear-to-row selection was practiced in each of four isolated plots. Beginning with the tenth generation alternate rows were detasseled, and seed was saved only from the highest yielding rows. After twenty-five generations yielding ability was disregarded.

The number of individual ears analyzed in each strain was variable for the first nine generations. From the tenth through the twenty-eighth generation, 120 ears were harvested for analysis in each strain, and the 24 most extreme ears were used to

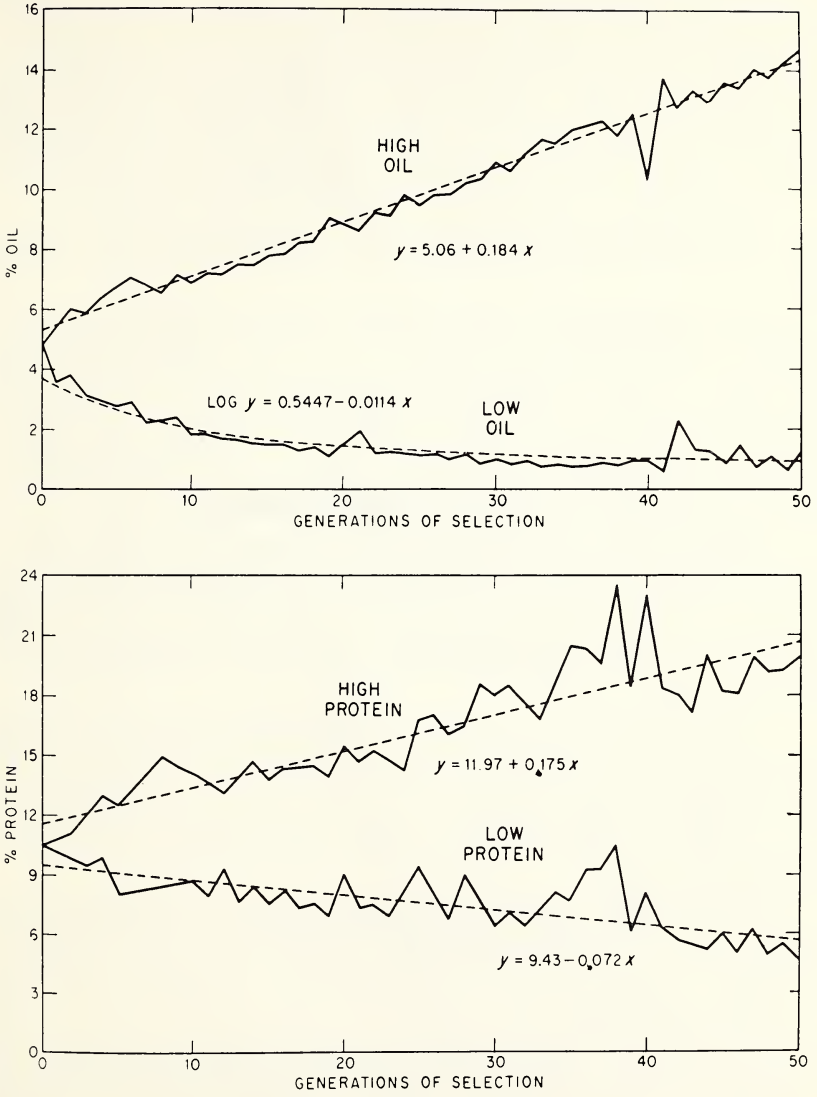


Figure 24 Effects of 50 generations of selection on oil and protein content of corn. Actual data are indicated by solid lines; fitted trends are shown by broken lines. (From Woodworth et al. 1952)

plant the following year's isolated plot.

From the twenty-ninth generation, the method was changed to obviate the difficulty of finding isolated plots. The number of ears harvested for each strain was reduced to 60, and the 12 ears at the extreme in the desired direction for each character were saved for seed. These were divided into two groups, each consisting of seed from six ears, and the seed bulked within the group. Crosses were made by hand-pollination between the two sources of seed for each of the four methods of selection.

The results of analyses were placed on a moisture-free basis. Diagrammatic presentation of the data is given in Figure 24.

In the diagram the solid lines represent actual data and the broken lines indicate trends. There have been rather wide deviations in different seasons. In general, however, there has been rather consistent progress in the direction of selection for High Oil, High Protein, and Low Protein. For the Low Oil strain there has been little if any progress in the direction of low oil from the thirtieth to the fiftieth generation.

Student (1934-35) attempted to estimate the number of genes in the selection experiment based upon the results for oil content. His conclusion is of considerable interest. He thought the results could be explained by the presence or absence of 20 to 40 genes, and possibly by 200 to 400 and not likely of the order of 5 to 10.

These results of selection for high and low oil percentages are of interest as a background of information in relation to studies of Sprague and Brimhall (1950) of recurrent selection as a means of increasing oil content. In their study they used a cross of Illinois High Oil x wx Os420. Results are presented diagrammatically.

The method consisted of analyzing ears for oil content and making crosses between progenies of the ears of most extrme oil content. From these bulked progenies individual selfed ears again were analyzed.

In the diagram (Fig. 25) the original and two cycles of selection are given. The vertical solid lines represent means of the population of ears tested, and the vertical dash lines represent the mean of ears selected, on the basis of oil content, to use in crosses for the following generation. In the first cycle the mean for oil content was a little higher than the mean of the original selfed ears. Likewise, for the second cycle variability for oil content, as represented by the curve of variability for

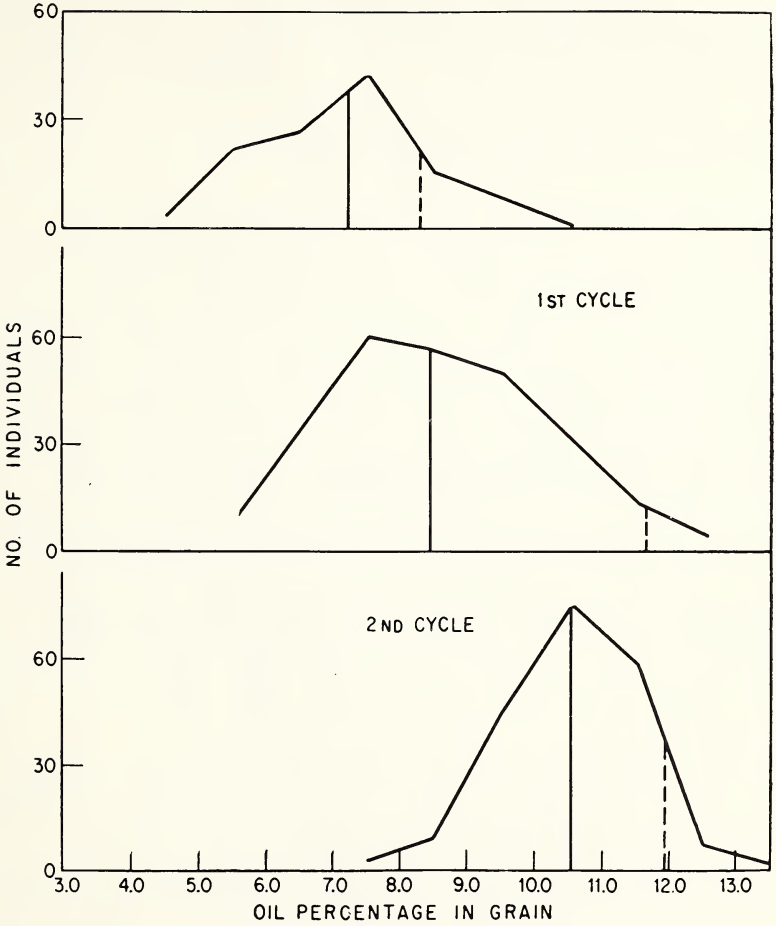


Figure **25** A comparison of frequency distributions of oil percentages in the corn kernel. Above: in the original population, Illinois High Oil x wx Os420; and center and below respectively, after one and two cycles of recurrent selection. (*From Sprague and Brimhall* 1950)

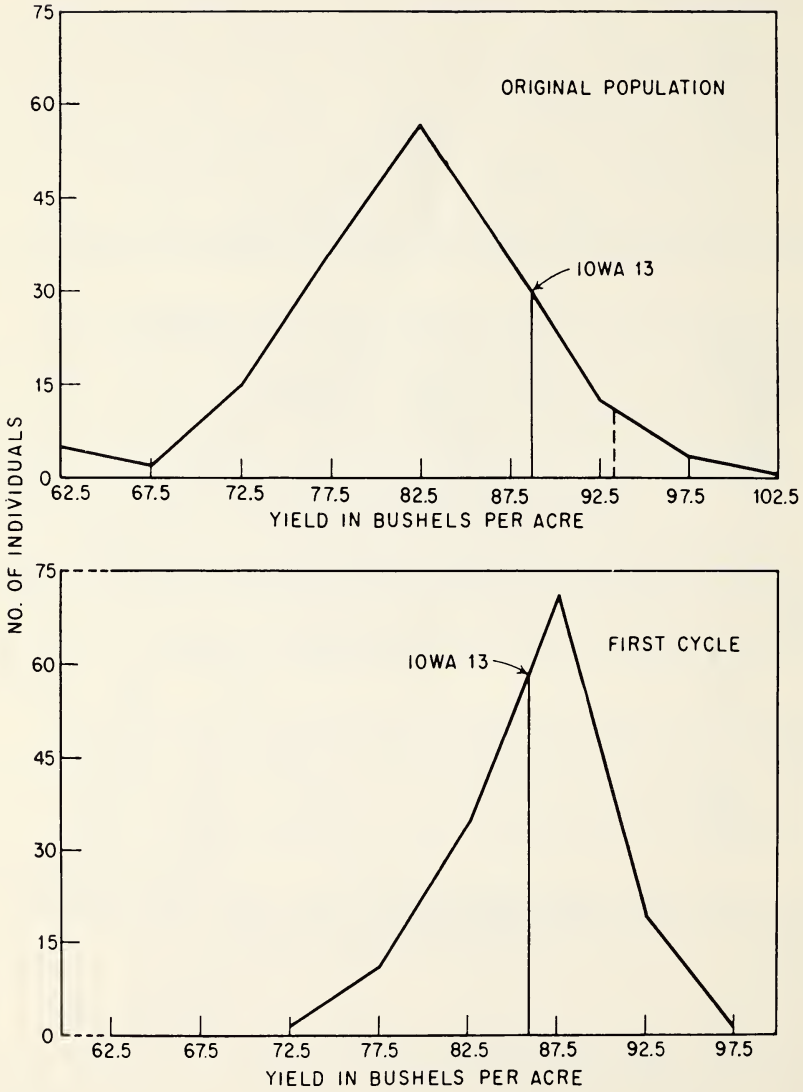


Figure **26** A comparison of the frequency distribution for yield in bushels per acre for top crosses from the original stiff-stalked synthetic and after one cycle of selection. (*From Sprague and Brimhall* 1950)

oil content in the second cycle, indicates that further progress could be made in cycle 3. The progress by two cycles of recurrent selection was very great. Two cycles of recurrent selection for oil content gave results equivalent to thirty generations of selection as practiced in the long-time selection experiments for chemical characters as carried out by the Illinois Agricultural Experiment Station.

It is of interest that the original material consisted of reciprocal backcrosses involving the single cross Illinois High Oil x wx Os420.

These results are in contrast to those obtained for recurrent selection for yielding ability using a stiff stalked synthetic produced in Iowa by combining inbreds that excelled in standing ability. Plants of this material were selfed, and outcrossed to Iowa #13. After carrying out the top-cross yield trial, seed of the best ears of 12 selfed progenies was used to make intercrosses. This seed was bulked and multiplied by sib-pollination.

The comparison of frequency distributions for yield of the original top-crosses and of those tested after the first cycle of selection is shown diagrammatically in Fig. 26.

The variability of the original first top-crosses was much greater than that of top-crosses tested after one cycle of selection. While the first cycle trial led to a much higher mean yield in its top-crosses, the range of variability in a plus direction was even less than that of the top-crosses of the original population.

After recurrent selection it should be emphasized that pedigree breeding by continued selfing is essential to isolate inbreds to use in three-way or double crosses.

Lonnquist (1951) used early testing to study the isolation of high and low yielding synthetics from Krug yellow dent. These two synthetics originated from S_1 lines of the Krug variety that were tested for combining ability in crosses with the Krug variety. The frequency distributions given in the diagram, Fig. 27, illustrate the effectiveness of early testing in isolating synthetics.

Lonnquist (1950) studied the combining ability from S_1 through S_4 generations of lines derived from sources that differed materially in combining ability. The original source material consisted of 36 S_1 lines from 200 S_0 plants of Krug selfed in 1942. Thirty-six selfed plants stood up well at harvest. These plants were evaluated in top-crosses with the original strain of Krug from which they were obtained. Eight lines

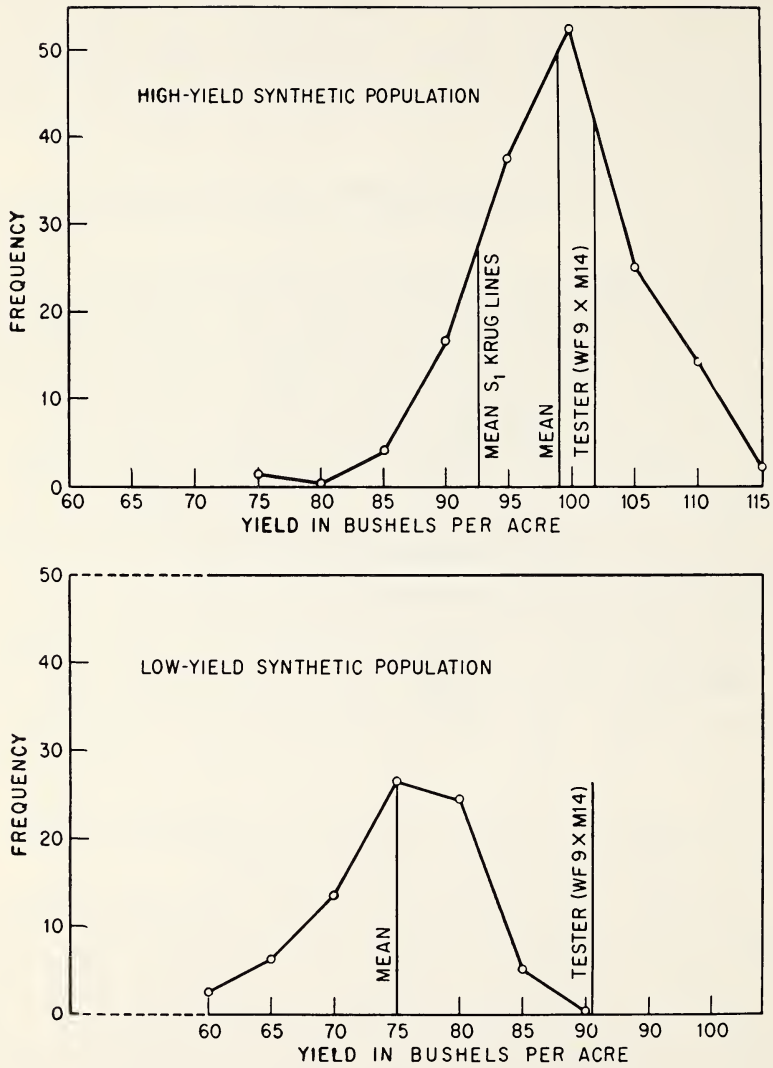


Figure **27** Frequency distributions of yields of (upper diagram) 152 top-crossed plants from a high-yield synthetic (1948), and (lower diagram) 77 top-crossed plants from a low-yield synthetic (1949), each synthetic population originating from S_1 lines of the Krug yellow dent variety. (*From Lonnquist* 1951)

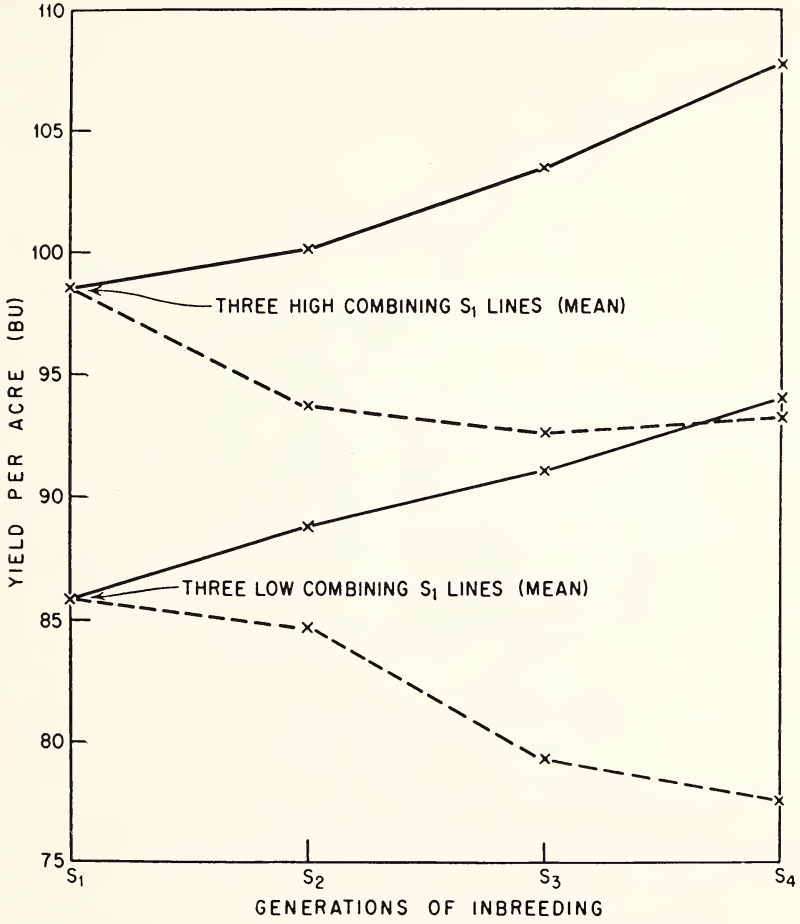


Figure 28 Comparative mean top-crossed performance of three high- and three low-combining S_1 lines of Krug and their respective high- and low-combining segregates, S_2 to S_4, selected for divergent top-cross performance in each generation. (*After Lonnquist* 1950)

from the upper yield range and seven from the lower were selected for further study.

From both the original high group and from the low, high and low combiners were chosen to initiate selection in a divergent direction. High or low combiners were selected in subsequent generations from S_2 to S_4 inclusive, depending upon whether the first selection was for high or low combining ability. Comparative mean performances are given in Fig. 28 for three high and three low combining lines of Krug, and for combining studies in S_2 to S_4 inclusive.

Lonnquist wrote as follows, "Although it has been demonstrated that the combining ability of a group of lines, or families, remains relatively stable from the S_1 through subsequent selfed generations, it has not been stated directly nor implied, as indicated by some, that segregation for yield in the early generations of in-breeding is non-existent." However, as discussed previously, Jenkins did maintain that the lines were relatively stable and Richey and Immer, from analysis of Jenkins' data could not substantiate Jenkins' conclusions.

From the diagram one may note that in S_4, the S_1 low lines, that in S_2 to S_4 were selected for high combining ability, slightly exceeded in mean yield the S_1 high combining lines, that from S_2 to S_4 were selected for low combining ability even though the number of plants tested in each generation was not large. The divergence of viewpoint of Richey and Jenkins, as explained previously, was regarding the relative stability for combining ability of Jenkins' inbreds when results of S_1 and subsequent selfed generations were compared. In this and other cases all that is important is to understand that relative stability seems to mean that original S_1 lines of high combining ability will give progeny in subsequent selfed generations of marked superiority in combining ability, on the average, to that of S_1 lines of low combining ability.

Lonnquist (1953) selected four low combining lines and five high combining lines, based on test crosses with (Wf9 x M14) after each generation of selfing from S_1 to S_4. Progressive selection for high or low, respectively, was made depending on classification of the original selection. These lines should be distinctly different after this extensive test. All possible crosses then were made between the nine lines and their crosses studied in yield trials. The results of this study are summarized as averages (See Table 28).

Table 28 Average Yield of Inbreds, and of Their Crosses; for Four Lines Classified as Low Combiners and Five of High Combining Ability as Determined from Test Crosses through S_1 to S_4. Bu. per Acre

		Lines Classified as	
		High	Low
Average Yield of Inbreds		59.4	33.4
Lines Classified as	High	91.9	
	Low	82.1	70.2

In these studies High x High on an average yielded 9.8 bushels more than High x Low, and 21.7 bushels more than Low x Low. The inbreds yielded relatively well, the five high combining inbreds averaging 59.4 bushels and the four low combining inbreds 33.4 bushels, the difference being 26.0 bushels. The inbreds were selected for combining ability but not for yield as inbreds. It is interesting that the high combining inbreds proved also to be markedly superior in yield as inbreds, to low combining inbreds. These results are consistent with earlier reviews regarding yields of inbreds and the average yield of their crosses.

Early Testing and Recurrent Selection in Producing Synthetics

Lonnquist and McGill (1956) have studied the use of early testing and recurrent selection in the development of synthetic varieties. They refer to the paper of Kinman and Sprague (1945) who studied various relationships between the numbers of inbreds that are combined to produce the synthetic and the expected performance of Syn 2, and later generations. These may be better understood by considering some of the questions previously clarified under a discussion of Synthetic Varieties (See pages 118-121). The expected yield from combining inbreds depends upon the average yield of all F_1 crosses between these, and the average yield of the inbreds. Subtracting the average yield of the inbreds from the average yield of all possible crosses between them, gives the average increase in

yield due to heterosis. If this is multiplied by n - 1/n, where n is the number of inbreds combined in the synthetics, one obtains an estimation of the value of heterosis to be retained in F_2. By adding this to the average yield of inbreds one obtains an estimation of the expected yield in F_2.

Actual experiments, involving propagation of different F_2 populations as synthetics, are essential to a solution of the problem. It seems evident that from any one study it is possible only to decide, for the group of inbreds used, how many should be combined to produce the most promising synthetic.

Kinman and Sprague suggested the use of S_1 lines as one means of obtaining higher yielding synthetics. Lonnquist and McGill (1956) present data from studies of early testing and recurrent selection relating to this problem. It would seem that with this method, however, the origin of the S_1 lines deserves consideration. Perhaps several origins would be more beneficial than the use of lines from a single variety source. The data as given, however, are very valuable.

The general procedure for producing Syn 2 for several synthetics studied was to test 100 to 165 S_1 lines using a tester which provided a broad genetic base (usually another synthetic). The number of S_1 lines used as basic material for the combination depended somewhat on the results and varied from 10 to 15 per cent of the tested sample. For the Krug material the original strain of Krug was used as a tester.

In the first study of three synthetics, to be presented, the yield and other characters of the original open-pollinated variety were taken as 100. The first and later cycles of recurrent selection are designated by subscripts where $Krug_1$ is the first

Table 29 Relative Performance of the Open-pollinated Varieties and Three Synthetics Expressed as Per Cent of the Parental Population taken as 100.

Population	Grain Yield	Moisture at Harvest	Lodging		No. of Tests
			Root	Stalk	
	Per cent	Per cent	Per cent	Per cent	
Parental Variety	100	100	100	100	
$Krug_1$, Syn 2	122	91	45	120	3
$Reid_1$, Syn 2	109	96	32	86	2
$Dawes_1$, Syn 2	113	109	---	47	5
Average	113	99	38	84	-

cycle synthetic made up of selected S_1 lines from Krug Yellow Dent, and $Krug_{11}$ would represent a second cycle synthetic made up of selected lines from Krug.

Results from first cycle synthetics are given in Table 29.

These results show that, on the average, the synthetics yielded 13 per cent higher than the open-pollinated varieties, with about the same moisture per cent at harvest, and were somewhat superior to the open-pollinated varieties in ability to withstand both root and stalk lodging.

From a test in western Nebraska a Dawes Syn 2 was compared with the Dawes variety, and with several hybrids as summarized in Table 30.

Table 30 Performance of Open-pollinated Dawes, Dawes Syn 2, and Twenty-eight Double-cross Hybrids at Two Locations in Western Nebraska

Kind of Corn	Acre Grain Yield	Moisture at Harvest	Stalk Lodging	Dropped Ears
	Bu.	Per cent	Per cent	Per cent
Dawes O P.	73.8	20.3	5.2	0.4
Dawes, Syn 2	80.5	22.0	3.4	0.0
Mean 28 Hybrids	76.1	20.0	2.0	0.3
Range of Hybrids	54 - 86	14 - 26	0 - 6	0.0 - 2.4

These results indicate definitely also that synthetics may be expected to perform better than the open-pollinated variety from which they are selected and in some comparisons equal to or better than comparable double crosses.

The yield of advanced generation synthetics is of interest also. Advanced generations Syn 2, Syn 3, etc., were produced from isolated plantings containing 5,000 to 10,000 plants. Ears from the better 150 to 200 plants were selected and the seed was bulked and used in advancing the synthetics. The performance of a given synthetic was evaluated after two generations of synthesis, which would be following the first segregating generation of the material evaluated.

Three advanced generations of the Krug synthetic were compared in 1949 with the double-cross hybrid U.S. 13 in replicated trials at eleven locations. The results are presented diagrammatically in Fig. 29. The synthetics were somewhat ear-

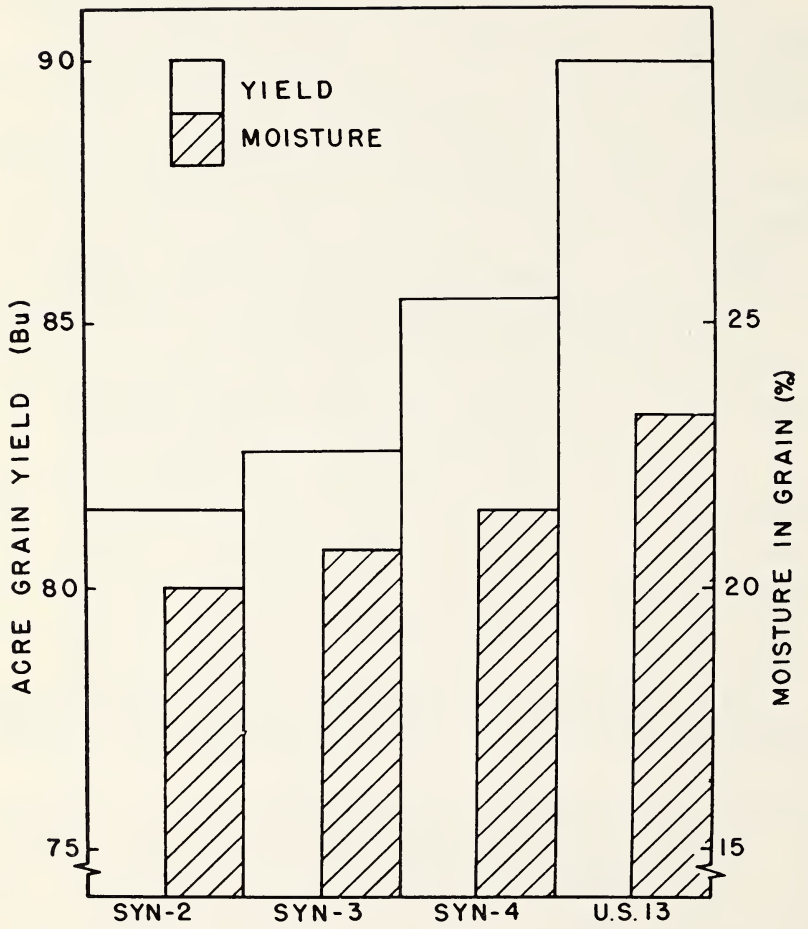


Figure 29 Relative performance of three generations of synthesis of Krug1 synthetic and hybrid U. S. 13 in eleven locations in 1949. (*After Lonnquist and McGill*, 1956)

lier in maturity than U. S. 13, had a lower moisture content at husking and a lower yield. There is some evidence of progressive improvement in yield from Syn 2 to Syn 4, presumably as a result of visual selection under open-pollinated conditions. However, with an increase in yield there is a corresponding increase in moisture percentage of the grain at husking.

Similar results were obtained by Lonnquist and McGill (1956) for advanced generation synthetics with visual selection compared in the Lincoln, Nebraska area during 1950-1953. See Table 31.

Table 31 Relative Performance of Four First Cycle Synthetic Varieties in Advanced Generations of Synthesis with Visual Selection

Generation of Synthesis	Population									
	$Krug_1$ (5 tests)		A_1 (5 tests)		B_1 (3 tests)		$Reid_1$ (2 tests)		Means	
	Yield	Moisture	Yield	Moisture	Yield	Moisture	Yield	Moisture	Yield	Moisture
	%	%	%	%	%	%	%	%	%	%
Syn-2	100	100	100	100	100	100	100	100	100	100
Syn-3	103	103	108	108	120	95	104	103	108	102
Syn-4	105	105	104	112	126	98	---	---	111	105
Syn-5	106	106	110	105	---	---	---	---	108	105

These results need not be summarized in great detail. For three of the synthetics (Table 31) $Krug_1$, B_1, and $Reid_1$ there was some indication of an increase in yield from Syn 2 to later generations and also a corresponding increase in moisture percentage. Thus for $Krug_1$ with the yield and moisture percentage at husking taken as 100 the yield and moisture percentage of Syn 5, were both 106. For Synthetic A_1 the yield percentage of Syn 5 was 110 and moisture percentage 105. For Synthetic B_1 there was marked improvement by two generations of visual selection where the results for Syn 4 for yield were 126 and for moisture percentage 98. These results give adequate proof that in these experiments under conditions where visual selection of desirable plants was practiced in advancing the generations, later generations may be expected to maintain as desirable performance as Syn 2, and in some cases there may be improved performance.

Chapter 16 PRODUCTION AND DISTRIBUTION OF HYBRID CORN SEED

The Important Work of Hybrid Seed Producers

As has been mentioned previously, the introduction of hybrid corn has greatly changed the problems of seed production. Large and smaller seed producers have developed interesting and valuable procedures for seed production. These include mechanical methods of harvesting hybrid seed, excellent drying facilities, and mechanical methods of shelling, processing, grading, and treating seed for the control of seed borne diseases. Desirable marketing and sales procedures have made high quality seed of adapted hybrids available to all growers. The problem of what hybrid to grow and what grade of seed to buy seems to be a major question that is faced by each corn grower. It is desirable to emphasize again the great value to the corn grower that results from having available a constant supply of high quality seed, adapted for each environmental condition. High quality seed is perhaps of as great importance as high yielding hybrids with desirable agronomic characteristics and plays its part as a major cause of increased yields obtained by the grower, as compared with methods used when open-pollinated varieties were grown primarily.

The development of present day methods of artificially bin drying seed corn has been of great value to the hybrid seed corn program. Drying of seed with artificial heat and fans of one kind or another dates from the early 1900's. The bin method of drying with using fans of ample capacity to move air through the bins at a rate of 40 to 50 feet per minute, with temperature controlled when the air leaves the fan at about 105°F., proved desirable. Seed corn quality was not injured even though the

moisture percentages were reduced down to 5 to 6 per cent. An early study by Harrison and Wright at Wisconsin was published in the American Society of Agronomy Journal in 1929. Prof. A. H. Wright, Emeritus Professor of Agronomy, with coworkers first tested a small commercial dryer in the old Agronomy Building at Wisconsin in 1926. Three commercial dryers were built also in 1926 by Wisconsin seed producers. Wright emphasizes the cooperation of other members of the Experiment Station Staff at Wisconsin, and of commercial seed producers, in carrying out the studies. Wright writes, "These early dryers became demonstration dryers, and since they worked out satisfactorily, the idea spread rapidly, and was generally accepted."

The part played by the large seed companies in the production, introduction, and popularization of hybrid corn, was explained rather adequately by Crabb in the hybrid corn history entitled "The Hybrid Corn Makers, Prophets of Plenty." Some students of hybrid corn history may conclude that the importance of the work of these larger companies has been somewhat overemphasized and that the work of the Experiment Stations and of smaller seed growers of Station recommended hybrids deserves somewhat greater emphasis. Be that as it may, there is universal agreement that these larger seed companies have carried out an excellent, extensive, and worthwhile business and that for the most part the seed produced has been a rather uniformly desirable product.

Because of Crabb's extensive and detailed review of the work of the larger seed producers, that part of the story will not be presented in great detail.

In the Corn belt, four of the larger seed companies are Pioneer Hi-Bred Corn Company, with headquarters at Des Moines, Iowa, Funk Brothers Seed Company at Bloomington, Illinois, Pfister Associated Growers and the DeKalb Seed Company at DeKalb, Illinois. Each of these companies has extensive hybrid corn testing programs throughout the Corn Belt and seed production plants for handling seed of various hybrids in different regions.

Henry A. Wallace seems to have been the early motivating spirit of the Pioneer Hi-Bred Corn Company and took an active part in its early organization. Copper Cross, a single cross, was one of the early hybrids that seemed outstanding, the first sale of this seed being made in 1924. This cross was between an inbred of Bloody Butcher developed by Richey and one of the Connecticut Leaming strains from Jones that was developed by

East and the writer. According to Crabb's story, fifteen bushels of seed were sold at a dollar per pound, or $56.00 per bushel.

In 1926 the present Pioneer Hi-Bred Seed Company was organized by Wallace and two friends, Newlin and Cassady. Mrs. Wallace aided extensively in financing this company. Raymond Baker joined the Pioneer Hi-Bred Corn Seed Company in 1928 and became director of research in 1933. His leadership, both in the breeding and production phases, is widely recognized. This company has maintained an outstanding research program from the beginning, in addition to very satisfactory testing, breeding, and producing programs, and the sale of adapted hybrids.

The Funk Brothers Seed Company at Bloomington, Illinois, was one of the leading producers of seed corn prior to the advent of hybrid corn. The corn breeding program of the Federal Field Station of the United States Department of Agriculture, operated in the fields and laboratories of this company, as was stated previously, was under the leadership of James R. Holbert. While the Station was adequately staffed with research leaders by the United States Department of Agriculture, it was also aided in many ways by the Seed Company. Under these conditions, early hybrids produced and tested by the Federal Field Laboratory were of great importance as a source of desirable hybrids that were introduced and sold by Funks. In 1929 about 2,000 bushels of hybrid seed were sold by this Company. When the Federal Field Laboratory was closed in 1937, Holbert returned to work with E. D. Funk as Vice-President in charge of research. For many years the continued research and leadership of Holbert played a leading role in the success of the Funk Brothers hybrid seed corn program.

The story of Pfister's early inbreeding and crossing program has been outlined previously. It is mentioned again here since the two earliest hybrids of outstanding performance that were produced and marketed resulted from crosses of single crosses of Holbert's, with single crosses from Pfister's, produced from inbred lines of Krug Yellow Dent. This led eventually to the rather large hybrid seed program of Pfister's Associated growers.

The DeKalb Agricultural Association, Inc., DeKalb, Illinois is one of the so-called big four hybrid corn seed companies. According to Crabb's story, the first large seed crossing plot of DeKalb was 75 acres grown in 1934. Because of the severe drought that year, only 325 bushels of seed were processed and

sold from the crop produced on this acreage. In 1935, however, nearly 15,000 bushels of hybrid seed was produced and sold to corn growers. Prior to 1937 Mr. Ralph Gunn was the leader of corn breeding work for DeKalb. Ralph St. John, who for many years previously was one of the project leaders in corn breeding at Purdue joined the DeKalb organization to take charge of breeding full season hybrids for the Corn Belt. Since that time Mr. Gunn has had charge of breeding work with early hybrids. Both Gunn and St. John deserve credit for the success of the DeKalb breeding program.

Because St. John aided so greatly in the DeKalb seed program, it is appropriate at this point to describe the early Purdue studies. Hybrid corn breeding in Indiana was initiated under the leadership of Dr. G. N. Hoffer, of the Botany Department, who was greatly influenced by Jones' work at the Connecticut Station in New Haven. Even today at Purdue a large part of the hybrid corn program staff is officed in the Department of Botany and Plant Pathology. At Purdue, however, there is very close cooperation between plant geneticists and plant pathologists, and for a visitor it is often not clearly evident which department is concerned, as many seminar, discussion periods, and research projects are carried on cooperatively.

Several of the men who have contributed greatly to the Purdue breeding program are John Trost, B. H. Duddleson, Ralph St. John, and G. N. Smith. Each of these men started work under the leadership of Dr. Hoffer. Trost and St. John sent out hybrid seed for testing in 1926.

John Trost in later years developed his own hybrid seed business and has produced single cross seed for sale to seed producers. He is an enthusiastic research student of hybrid corn and is known not only for his leadership at Purdue but also as a breeder and producer of hybrid seed.

Glenn Smith, for many years Associate Geneticist of ARS, United States Department of Agriculture, has been an outstanding leader in sweet corn improvement. His headquarters were in the Botany and Plant Pathology Department of Purdue University. Golden Cross Bantam is a single cross that is resistant to bacterial wilt, yields well, and has excellent quality for canning, freezing, and for home gardens. It was first made available to commercial seed growers in the spring of 1932. Small quantities of Foundation seed of the two inbreds known as Purdue 51 and Bantam were maintained at Purdue University. Circular No. 268, 1933, by Smith, describes the early studies of sweet

corn breeding and gives a description of the development of Golden Cross Bantam. Smith furnished a statement from the Agricultural Marketing Service for 1957. The total production of hybrid sweet corn seed was 11,924,423 pounds, and of this total, 1,575,330 pounds of Golden Cross Bantam seed was produced. This is somewhat larger than the total production of 1,295,620 pounds of all types of open-pollinated sweet corn seed.

The early leadership of Dr. Hoffer has been outlined briefly. Dr. Hoffer emphasized the importance of proper fertilization. He devised methods of determining the needs of plants for various nutritional factors by means of plant tests. He emphasized also the value of using crosses that produced uniform genetic material in his nutritional studies as well as in studies of reaction to disease organisms.

At a meeting of the National Canners Association in January, 1926, Dr. Hoffer gave a talk on "Hybrid Sweet Corn." Ward Cosgrove, of the Minnesota Valley Canning Company, was impressed, but thought at first that Hoffer was nature faking. Dr. Hoffer soon convinced him that hybrids would be of great value to the sweet corn canner. Jack Barnard was sent by the Company to visit Hoffer and learn more of the breeding methods used. Hoffer advised Barnard to contact the writer at University Farm to obtain information from the Minnesota Station regarding the newer methods of corn breeding.

Without doubt similar results have been obtained in many other states, but the Minnesota story well illustrates the developments that resulted from improvements in breeding methods.

As a result of the visit in the spring of 1926 by members of the Minnesota Valley Canning Company with corn breeders at the Minnesota Station, a cooperative project was drawn up that year with the approval of the Minnesota Station Administration for the breeding of sweet corn.

At that time the variety of corn grown by the canning company was called Del Maiz. It had resulted from selection of a cross of Golden Bantam with Stowell's Evergreen. It resembled the Evergreen parent in plant habit and the Bantam parent in seed color. The corn breeders at University Farm, at that time consisting of the writer and H. E. Brewbaker, agreed to supervise unofficially the breeding program at LeSueur to the extent desired by the Minnesota Valley Canning Company. In return for this aid the canning company made available a fund of $1400 to aid in sweet corn breeding studies at University

Farm, and to be spent as seemed most desirable to the project leaders. Dr. H. L. Thomas, now a member of the Agronomy and Plant Genetics Department at University Farm, was the first half-time research assistant financed by the fund from the canning company.

Dr. Hoffer kindly made available inbred material from the Purdue project. One phase of the work at University Farm consisted of studies of reaction to smut carried out cooperatively by the corn breeders and plant pathologists. Under Minnesota conditions some of the inbreds from Purdue proved highly susceptible to smut. However, a few Purdue lines were resistant. Two of these inbreds were used in a single cross that for several years was canned on the ear by the canning company.

Over 1,000 ears were selfed at University Farm in 1926, and of these 560 were continued in 1927. Most of the work at University Farm was with three varieties, Golden Bantam, Country Gentleman, and Crosby. During the next few years the money received from the canning company was used chiefly to pay the salary of a research assistant, although a few hundred dollars were used for field and laboratory expenses.

An anniversary book of the Green Giant Company describes the start of the breeding work with corn in 1926, cross breeding results in 1932, and the addition of skilled agricultural technicians in 1940 to carry out studies in soil fertility, plant physiology, plant pathology, and insect control, in addition to extensive continuous studies of breeding and related problems of field and laboratory evaluation.

Today the Green Giant Company operates cannery locations in 22 areas, eight in Minnesota, four in Wisconsin, one in Iowa, two in Illinois, one each in Idaho and Delaware, three in Washington State, and two in Canada. Seed for planting results from the breeding studies carried out at Le Sueur. Single crosses are used for the main crop, the seed production being carried out in Idaho. While the Green Giant Company has conducted its own breeding program, it seems evident that the Minnesota Agricultural Experiment Station researches played an important part in the initiation of the program and in aiding in some of the technical phases. Hybrid corn has proven of great value because of the uniform, high-quality product that has resulted. Of course, many other phases of applied technology also have been essential to the success of the program.

Among the early companies that have long been interested in hybrid seed corn, the Northrup King Company, of Minneapolis,

should be included. The work of this company is well known to the writer because in the early days the Minnesota Agricultural Experiment Station research staff was consulted freely by the Northrup King research staff. In relation to breeding phases, the writer and asociates from the beginning shared their research experiences and viewpoints with specialists of the company.

Under the leadership of C. A. Bush, selection in selfed lines was started in 1921 with 1,000 selfed ears of Minnesota #13, of which 277 progenies were grown in 1922. Their first crosses of inbreds were made in 1925. In 1933 about 300 acres of crossing plots were grown with about 10,000 bushels of seed produced and sold.

Besides working with field corn, where originally most of the important Minnesota varieties have been used as a source of germ plasm, Northrup King Company has drawn on many other sources in much the same manner as followed by the Minnesota Agricultural Experiment Station corn breeders. Studies were started with Golden Bantam sweet corn in 1922 and 27 other varieties were also included. The first production for sale was an 8-rowed Bantam cross for the market gardener, first available in 1931. Both market garden and canning types of hybrid sweet corn have been produced.

About 1950, Dr. F. G. Holdaway, Entomologist of the University of Minnesota, was employed as a Consultant to help in organizing studies designed to produce inbreds and hybrids resistant to the European corn borer.

The Northrup King Company has become Minnesota's largest producer of hybrid seed corn. They have six separate seed plants in the Corn Belt, four in Minnesota and two in Iowa. They have specialized in maturities for northern areas of the Corn Belt. Their main breeding stations are near Minneapolis, at Hampton, Iowa, and at Washington, Iowa. As with the Green Giant Company, the production of hybrid sweet corn seed is carried out in Idaho.

Cargill Incorporated, of Minneapolis, a large grain company, has handled hybrid corn since the mid-thirties through its seed division.

In 1946, Cargill purchased the Nicollet Hybrid Seed Company of St. Peter, Minnesota, and set up a Hybrid Corn Department in its organization. In 1947, they added the Ahrens Hybrid Corn Company, Grinnell, Iowa, and have steadily increased in size since. Today their hybrid corn seed production is handled

in five production areas in the Corn Belt at St. Peter, Minnesota; Grinnell and Mt. Pleasant, Iowa; Aurora, Nebraska; and Pontiac, Illinois.

In addition, since 1947, Cargill Inc. has been pioneering with hybrid corn in the Argentine and today produce and sell well over half of the hybrid corn seed used in Argentina.

Cargill's corn breeding research center is at Grinnell, Iowa, with sub research stations at St. Peter, Minnesota; Aurora, Nebraska; Rochelle and Tuscala, in Illinois; Homestead, Florida; and Pergamino, Argentina.

There are many hybrid seed corn producers in various states. No attempt will be made to discuss the scope of work of many of the individual companies. It seems desirable to outline briefly the development of work of a few of the major seed producers of hybrid corn in several southern states.

P. H. Harvey, Head of the Field Crops Department at Raleigh, North Carolina, made available a brief history of McNair's Yield-Tested Seed Company that was prepared by Mr. K. J. Shaw, Executive Vice President of that company. The following is quoted from K. J. Shaw's history.

"McNair's Yield-Tested Seed Company, Inc. was organized in 1947 and is a wholly owned subsidiary of John F. McNair, Inc., a farming and mercantile firm with extensive land holdings in the south central part of North Carolina. Agricultural crop seed of various agronomic crops are produced on approximately 5,000 acres of McNair owned land and marketed by McNair's Yield-Tested Seed Company. The Seed Company sells only seed produced on McNair farms to the Wholesale and Dealer trade in eight Southern States.

"Hybrid seed corn production has grown from a small acreage in the early forties to an average annual production of 2,000 acres. Four thousand acres is the maximum ever grown in one season. Facilities for processing and storing all seed grown are located on the Aberdeen Road North of Laurinburg, North Carolina.

"Prior to 1958, hybrid seed corn production consisted of hybrids developed by Public agencies and certified by the State Crop Improvement Association. In 1958, several McNair hybrids developed by their own research staff during the past twelve years were introduced for commercial sale. In addition, McNair's Yield-Tested Seed Company is sole producer of "Table Joy" hybrid sweet corn, a superior sweet corn developed in co-

operation with Dr. H. S. Perry, Botany Department, Duke University, Durham, North Carolina."

P. H. Harvey also obtained information on the Farmer's Cooperative Exchange hybrid corn program from Mr. M. J. Wood, Director, Seed and Grain Production Division with headquarters at Statesville, North Carolina. The following is quoted from a letter written by Mr. Wood to Dr. Harvey:

"We began the production, processing and distribution of hybrids just as quickly as there was material available from the college that was adapted to the conditions in our state. We produced just a few top hybrids in the year of 1943. It was in 1944 that we built our first plant here at Statesville, and went into the production of hybrids on a sizable basis. This grew continually through the years from '43 and in the year of '48 it was necessary for us to build an additional plant, which was located at Washington, North Carolina, in order to take care of the demand we were having for hybrid corn. Our production of hybrids continued to grow on through the years until we reached a sizable acreage of approximately 800 acres, and processing and distributing approximately 30,000 bushels of corn each year."

A. A. Fleming, in charge of corn breeding at the University of Georgia, Athens, Georgia, prepared a summary of the history of Coker's Pedigreed Seed Company, Hartsville, South Carolina. This seed company is well known for its early and continued interest in seed improvement problems. The story as given here was written by Dr. Fleming.

"Plant breeding by Coker's Pedigreed Seed Company had its beginning in 1902 when W. C. Coker, a botanist at the University of North Carolina, made 30 plant selections out of Jones Improved cotton. In 1903, the selections were planted on the Coker farms in Hartsville, South Carolina, under the supervision of a botany teacher, D. N. Shoemaker. David R. Coker, a brother to W. C. Coker, took over the breeding work in 1904 and continued selection until the most outstanding strain was isolated. This strain was named Hartsville.

"In 1908, pioneer work was begun in the development of improved varieties of small grain followed by tobacco in 1927 and the development of adapted corn hybrids to the South in 1939. Major breeding work is now being done with cotton, small grain, tobacco, hybrid corn, and soybeans.

"In 1921, Mr. David R. Coker said: "We did not take up this business as a money-making proposition, but mainly because the condition of southern agriculture demanded that more

attention be given to the improvement of agriculture through breeding and introduction of better varieties of our staple crops and the maintenance of a reliable source of highly bred seed. When our work was started in 1902, no other work of similar kind had been started in the South. We are the pioneer pedigreed seed breeding company in the South."

Fleming also was responsible for furnishing the story of the Greenwood Seed Company, Thomasville, Georgia, although the information was made available to Fleming by W. H. Freeman, formerly of the Greenwood Seed Company.

"In 1945 Mr. John Hay Whitney, owner of Greenwood Farms, set aside these holdings to be used for the betterment of Southern agriculture. This was done initially under the supervision of Major L. A. Beard with E. V. and Roy Komarek as managers, and later as managers under Mr. Whitney on the death of Major Beard in 1954.

"The facilities of the plantation were placed at the disposal of the Georgia Coastal Plain Experiment Station. First seed production took place in 1945 with Florida W-1, a white hybrid developed by Fred H. Hull. The acreages were utilized for experimental hybrid production, yield testing, and foundation seed production. It was through the financing of Greenwood Farms that the foundation seed stocks for hybrid seed in Georgia was made available to other growers in the state and in the South.

"In 1948, the Georgia Coastal Plain Experiment Station released Dixie 18, a yellow hybrid adapted to the Coastal Plain. Greenwood Seed Company expanded production of this hybrid so that at one time the entire production of over 3,500 acres was devoted to this hybrid.

"Since 1953 Greenwood has established a corn breeding program and has developed several hybrids in keeping with one of its primary objectives, the betterment of Southern agriculture."

Another development of considerable interest in relation to the hybrid corn history consisted of the formation of several industrial companies devoted to the building of special equipment primarily designed to aid in the handling of the production and processing of hybrid corn seed. As an illustration we quote from a recent statement prepared by Robert M. Wolfe of Corn States Hybrid Service, Inc., Des Moines 14, Iowa.

Mr. Wolfe writes, "The new fledgling industry needed specially designed drying facilities to provide early harvesting, and slow gentle drying of the hybrid seed to preserve its pre-

cious germination before freezing weather. The Campbell Heating Company of Des Moines, Iowa were the first to recognize the importance of the gentle air drying, and as a result of their two-way reversed air system, 85% of hybrid seed corn is dried by the Campbell system.

"The Superior Company, Hopkins, Minnesota, were rapid in their engineering designs to recognize the importance of proper thickness, width, as well as length separations for uniform and accurate planting of the seed.

"Also, the industry needed new shellers to lessen seed coat damage, detasseling machines for economical and efficient carrying of detasseling crews through the fields. Another important product that represented a special project to the industry was the use of husking beds, inasmuch as the seed was harvested at high moisture content, and that a high percentage of husks were present on the harvested corn.

"As a result of the special problems, there was no central source of information in co-ordinated planning; another new industry came into its own in 1943. Corn States Hybrid Service, Inc., Des Moines, Iowa for the first time offered the mushrooming industry the advanced drying methods of the Campbell people, specially designed sizing flow incorporating the Superior equipment, their own design of husking bed, the introduction of Holden Foundation Seed, new fungicides such as Captan, which is so widely in use, pollinating supplies, and many other special products so badly needed, and today tries to offer the newest and latest of the special products needed for the finest quality of seed.

"Also, the Corn States personnel, by extensive travel and sampling programs, assisted the industry and our federal governmental agencies in the expansion of hybrid seed corn on a world-wide basis.

Studies at Experiment Stations and Seed Production in Various States

A summary of studies at various experiment stations in the United States has been made with the aid of investigators who have been, and who in many cases are today active leaders in corn improvement. A questionnaire was sent by the writer to workers at each of the stations and the summary given in Table 32 was taken directly from the replies received. It includes the

Table 32 Hybrid Corn History of Early Studies of Self-fertilization and Seed Sales in Various Corn Producing States.

State	Started selfed lines	Hybrid seed first sold by commercial companies	Proportion of Seed Sales				
			Initial 5 years after seed became available			Recent 5 years, 1956-60	
			Station hybrids Open-pedigrees[1]	Company hybrids Closed-pedigrees	Years	Station hybrids Open-pedigrees	Company hybrids Closed-pedigrees
Iowa	1922	1924	20	80	1931-35	4	96
Illinois	1920	1932	50	50	1933-37	5	95
Indiana	1917	1933	75	25	1933-37	35	65
Ohio	1920	1935	65	35	1934-38	25	75
Michigan	1921	1938	60	40	1939-43	25	75
Wisconsin	1923	1932	80	20	1936-39	33	67
Minnesota	1914	1933	90	10	1931-35	5	95
Nebraska	1909	1927	0	100	1927-31	15	85
Kansas	1923	1937			1941-45	10	90
North Dakota[2]	1927	1936-37	16	84	1936-40	25	75
South Dakota[3]	1927	1936	5	70	1944-48		
Missouri	1928	1930	1	99	1931-35	10	90
Kentucky	1920	1940	98	2	1936-40	15	85
Tennessee	1922	1939	90	10	1939-43	73	87
New York	1921	1932	95	5	1929-33	55	45
Pennsylvania	1943	1935	33	67	1940-45	45	55
North Carolina	1936	1937	48	52	1942-46	30	70
South Carolina	1946	1940	70	30	1946-50	25	75
Virginia	1928	1939	60	40	1939-43	30	70
West Virginia	1920	1933	0	100	1936-40	70	30
Arkansas	1937	1939				30	70
Georgia	1939	1940	90	10	1945-49	40	60
Florida	1927	1940	95	5	1941-45	75	25
Mississippi	1916	1940	5	95	1938-42	50	50
Texas	1927	1938	75	25	1942-46	80	20
Oklahoma	1930	1935	0	100	1935-40	5	95
Colorado	1921	1937	60	40	1938-42	2	98
Wyoming		1939	20	80	1939-43	30	70
California	1928	1944	0	100	1944-48	92	80
Connecticut	1905	1921	100	0	1921-25	0	100

[1]Open-pedigrees where the identity of the inbred parents is given, and closed-pedigrees where the inbred parents are a secret known only to the company concerned.

[2]During 1936-40 in North Dakota, Minhybrids from Minnesota are included in seed sales of commercial companies.

[3]In South Dakota the percentage of open-pollinated varieties for 1943-48 was 25 and in 1950-54 was 25. These percentages have been subtracted from 100 before calculating percentages of hybrids. Note that the data are for 1950-54 as given.

year that selection in selfed lines was started, and the year when hybrid seed was first sold by commercial seed producers. A comparison also is given of the proportion of seed sales, for the first five years when hybrid seed became available, of hybrids produced from station origin of open-pedigree hybrids and of hybrids produced by seed companies under the closed pedigree system. Information for the period 1956-60 inclusive is given also for the proportion of seed sales from these two origins.

In several states, notably Indiana and Wisconsin in the Corn Belt; Florida, Texas, Mississippi and Georgia in the South; Pennsylvania, New York and West Virginia, station hybrids, produced by Station breeders, have been and are being grown extensively. It seems difficult to the writer to explain in all cases why the corn producers of some states have used open-pedigree Experiment Station hybrids rather than closed-formula hybrids much more extensively than in other states. In the South the hybrids produced by Experiment Station research have continued to give excellent performance and seed companies in many cases have specialized in the production of open-pedigree hybrids. Similar causes may be the reason why in Pennsylvania, West Virginia and New York that open-pedigree hybrids continue to be grown so extensively. In the Corn Belt open-pedigree hybrids continue to be of considerable importance in Indiana and Wisconsin, perhaps because cooperation has been continued between special agencies of seed producers and the smaller and intermediate sized seed producer. Certain states in the Corn Belt, notably Illinois, Iowa and Minnesota, have made inbred lines and single crosses available to seed growers even before they are introduced as Station double crosses. These differences in the apparent source of seed, however, seem an interesting phase of the hybrid corn story. Information regarding the sale of seed in several states collected several years ago may serve to illustrate some of the problems and emphasize the many seed companies that are making hybrid seed universally available to the grower.

In Ohio, according to G. H. Stringfield, the number of growers of hybrid seed for certification was approximately 120 in 1957. Of these, twenty-eight produced seed from acreages of 15 or less, fifty producers had acreages from 15 to 61, ten had acreages above 61, ten had acreages above 61 and less than 200, six produced from 200 to 300 acres, and four had between 300 and 400 acres. Total acreage of certified hybrids was ap-

proximately 8000. At an estimated yield of 40 bushels of processed seed per acre, over 300,000 bushels of hybrid seed were produced and certified.

In Indiana, K. E. Beeson has given similar information for growers of certified seed. From a small acreage of 2 in 1933, there was a rapid increase to approximately 5000 acres in 1937, to over 7000 acres in 1940, and from 10 to 14 thousand acres up to 1957. Total production of seed of Station hybrids was estimated conservatively in the neighborhood of 500,000 bushels during these latter years.

N. P. Neal has furnished estimates of the corn acreage in Wisconsin consisting of over 2,500,000 acres during 1955 to 57 inclusive. He estimates also that one bushel of seed should plant six acres, on the average, and on this basis 450,000 bushels of hybrid seed would be needed annually. The acreage devoted to the production of station hybrids in the past five years varied from 7000 to 8000 acres. The estimate given of processed seed production of station hybrids approximates 340,000 bushels. Of this total, Dr. Neal estimates that approximately 220,000 bushels of seed of Station hybrids is planted annually in Wisconsin, the balance being merchandized in other northern states and in Europe. The following is quoted directly from Dr. Neal. He writes, "However, with the passing of the years and the changing economic and other circumstances, there has been a substantial reduction in the number of farmer seed producers. Probably a dozen major growers are responsible for 60 to 70 per cent of the total production. Even these operate as family enterprises. In 1957, there were 81 commercial producers of Station hybrids." Three of the larger growers produce closed pedigree hybrids. The Jacques Seed Company at Prescott, that sells both Station and closed pedigree hybrids, maintains a breeding and foundation seed stocks program.

The Station breeding programs of these three states, Ohio, Indiana, and Wisconsin, have been active in research on basic principles but perhaps no more so than in several other states where a much larger portion of seed sales consists of closed pedigree hybrids than is the case in these three states.

P. H. Harvey very kindly obtained information, at the request of the writer, prepared by John C. Rice, Director of the North Carolina Crop Improvement Association, regarding the production and sale of certified hybrid seed corn for three years based upon the total tags issued for bushel lots of seed. Data for 1955-56 and for 1957-58 seem of interest.

During the first year mentioned there was a total acreage of 10,695 while that of 1957-58 was 3,980 acres. There were 156 growers the first year, and a production of 17 hybrids, with a total bushel production of 209,238, while in 1957-58 there were 93 growers, 15 hybrids certified, and a bushel production of certified seed of 166,195. In 1955-56 there were five growers with over 500 acres each, five with 100 to 500 acres, and 146 with less than 100 acres. In 1957-58 there were two growers with over 500 acres, five with from 100 to 500 acres, and 86 with less than 100 acres. The state acreage planted to corn in 1955-56 was 1,969,000 acres and an indicated acreage for 1958 of 1,911,000.

A. A. Fleming of the University of Georgia has emphasized the importance of the double-cross hybrid, Dixie 18, that has been grown so extensively in the South. It was released in 1948 by the Georgia Coastal Plain Experiment Station and has occupied a larger acreage in the South than any other hybrid. In 1954, for example, there were 15,000 acres of certified seed-production fields of this hybrid in the South.

Fleming also supplied estimates relating to hybrid corn in Georgia in 1957. A total of 2,768,000 acres planted included an approximate acreage of Station bred hybrids of 1,550,080, of closed pedigree hybrids from seed companies of 664,320 acres and of open-pollinated corn of 553,600 acres. Fleming estimated that open-pedigreed hybrids were produced by 30 different seed companies or individuals with a total bushel production of hybrid seed of 155,008 bushels and that closed pedigree hybrids were produced by 10 different seed companies with a total production of 66,432 bushels. He estimated also that 55,360 bushels of open-pollinated seed was planted.

I. J. Johnson furnished information regarding the production and sale of hybrid corn seed in Iowa. According to their estimate about 175 different companies produce and sell hybrid corn seed. This includes the four large companies (Pioneer, DeKalb, Funk, and Pfister Associated Growers), about 12 companies of intermediate size, many smaller companies, and 46 open-pedigree producers of hybrid seed. Two companies, Clyde Black and Son, Ames, and Holden Foundation Hybrids, Williamsburg, are producers primarily of foundation single crosses.

The total bushels of hybrid seed produced annually in Iowa is estimated at 2 million bushels with planting needs of 1.6 million. In 1957, 280,742 bushels of certified seed was produced

and of this 121,061 bushels were Station hybrids.

J. H. Lonnquist of Nebraska has furnished information regarding the sale in 1956 of hybrid seed in that state. The estimates as made were obtained by a postcard survey made by Mr. Dreier, of the Out-State-Testing program, where every 10th farmer listed as a corn grower was contacted.

A total of 71 companies, or seed producers, were named and there were 759 hybrids mentioned. In 1956, Nebraska had approximately 6 1/2 million acres of corn. DeKalb, Pioneer, Cornhusker, Funk and Pfister Associated Growers sold the largest amount ranging from 145 thousand bushels to 70 thousand. Steckley, Cargill and Teckseed sales ranged from 45 to 26 thousand bushels. United-Hagie and Maygold each sold about 14 thousand bushels and the total sales of Certified Seed Producers was estimated as 51,600 bushels. Lonnquist writes, "Aggressive leadership and rapid growth resulted in turning to closed pedigree production, usually within a short time," as an explanation of the relative sales of closed pedigree hybrids and of Station certified hybrids. It is of interest that several of the companies of intermediate size that now produce closed-formula hybrids started as producers of certified seed.

E. C. Rossman estimates that a little over 250,000 bushels of hybrid seed are planted annually in Michigan. Certified hybrid seed of Station origin, of 9 different companies, totals about 32,000 bushels, or approximately 12 percent of the seed required. Of the 9 producers mentioned, five produced less than 2000 bushels, one slightly more or 2200 bushels, and three 6000, 6800, and 11,000 bushels, respectively. The remainder of the seed used for planting consisted of closed pedigree hybrids.

W. R. Findley, of ARS, United States Department of Agriculture, with headquarters at the Kansas State College, has assembled available information on sales of hybrid seed corn in Kansas. With the help of others, an estimate has been made that 80 percent of the closed pedigree hybrid seed is sold by Pioneer, DeKalb, Funks and Pfister Associated Growers. The more important smaller producers include Ed. F. Mangelsdorf and Bros., Cornelli Seed Company, Steckley Seed Company, Earl May Seed Company, United Hagie Hybrids, Inc., and Nichols Seed Company. In 1956 total seed sales for the above-mentioned seed producers was approximately 190,000 bushels.

The decline in numbers of growers and acreage certified in recent years is evident from the following comparisons. In 1953 there were 35 growers of certified hybrids with an acreage

of 2198. By 1955 the number of acres for 21 growers was 1576 1/2, while in 1957 there were only seven growers with 388 1/2 acres that were certified.

O. A. Ulvin, Supervisor, Section of Seed Inspection, State Department of Agriculture, furnished information based on the sale of seed tags, which led to the summary for Minnesota of bushels of hybrid seed produced for sale during the period from July 1956 to July 1957, inclusive. The seed tag sales accounted for 1,014,982 bushels which should be sufficient to plant approximately 6 million acres.

The bushel production for the four larger producers ranged approximately from 285 thousand to 103 thousand, and that of five other large producers ranged from approximately 40 to 28 thousand. The production of three seed companies ranged from approximately 18 to 11 thousand bushels, and there were seven companies with production ranging from 8000 to 5000 bushels. The remaining 22 companies had a total production of 18,415 bushels.

Information regarding the production of certified hybrid seed corn in Minnesota was supplied by Ward Marshall, Manager of the Minnesota Crop Improvement Association. This Association is charged with seed certification of farm crops.

For hybrid seed corn both open and closed pedigree hybrids are, according to methods as quoted from the 1958 Seed Certification Standards of the Crop Improvement Association, as follows:

> "The seed producer shall make an affidavit to the effect that the parent lines used in the commercial crossing plots are of the same breeding and purity as the parent lines used in the hybrid that was tested by the producer and registered with the State Department of Agriculture and upon which his affidavit is based.
>
> "Hybrids will be certified on the affidavit of the producer filed with the Minnesota Crop Improvement Association that the hybrids have been tested for at least three years by the producer and have given satisfactory yields compared with standard varieties of the same maturity, and are in all other respects desirable hybrids."

In 1957 there were 21,592 bushels of hybrid seed corn of open pedigree certified and 157,190 bushels certified for closed pedigree hybrids. There were 31 growers that produced only open pedigree hybrids, six that produced only closed pedigree hybrids and five that produced both open and closed pedigree hybrids.

Information from other states includes that from North Dakota, Kentucky, Missouri, Pennsylvania, Arkansas, and Florida.

According to William Wiidakas, there are three seed companies in North Dakota that produce, process and sell hybrid seed corn. Fargo Seed House, Fargo, North Dakota, produces between 20 and 30 thousand bushels of certified experiment station hybrids annually. Agsco Seeds, Inc., Grand Forks, North Dakota, produce about 40,000 bushels of hybrid seed annually, largely from inbreds and single crosses of station origin. Oscar H. Will & Co., Bismarck, North Dakota, an old company founded in 1855, has produced hybrid seed in recent years either from Station single crosses, or between Station single crosses with single crosses of their own production. There are more than 15 brands of commercial seed company hybrids sold in North Dakota. Kingscrost, N. K. Co., Funks, DeKalb, Pioneer, Pfister and Pride are leading companies. The production of hybrid seed has changed from the small individual farmer producer to the specialized company. Individual farmers often produce seed under contract with the seed company.

F. A. Loeffel has estimated the production and sale of 21 certified open-pedigree seed producers in Kentucky as approximately 60,000 bushels. He also estimates the sales of seed of closed-pedigree hybrids as totaling 175,000 bushels. This includes four out-of-state companies, Funk, DeKalb, Pfister Associated Growers and Pioneer with total seed sales estimated at 105 thousand bushels while six companies with headquarters in Kentucky sold approximately 70 thousand bushels.

C. O. Grogan, Agronomist, ARS, United States Department of Agriculture, stationed at the University of Missouri, furnished information regarding hybrid seed corn for Missouri. Missouri farmers plant between 3 and 4 million acres of corn annually.

The DeKalb Company produces between 60 and 80 thousand bushels of seed in Missouri annually and have a processing plant located at Marshall, Missouri. Other large companies selling hybrid seed in Missouri are Pioneer and Funk. The Missouri Farmers' Association located at Marshall produces around 100 thousand bushels of hybrid seed annually. In 1946, when production was around 25,000 bushels, most of the seed was of certified hybrids. This seed producing division in more recent years consists almost entirely of closed pedigree hybrids. At present there are approximately 25 different producers of cer-

tified seed, and this type of seed accounts for about 10 percent of the total sales.

According to L. L. Huber, hybrid seed requirements in Pennsylvania are about 200,000 bushels annually. Pioneer, DeKalb, Funk and Pfister Associated Growers are the larger companies. There are also three large farm cooperatives that handle hybrid seed corn, - The Pennsylvania Farm Bureau, G. L. F. and Eastern States Exchange, a few smaller cooperatives and 10 independent producers. Approximately half of the corn seed distributed in Pennsylvania belongs to the open pedigree category. Five of the largest producers in Pennsylvania are T. A. Doebler & Son, Hoffman Seed and Grain Co., Seem Brothers, George Weaver and George Sherwood who grow an average of about 300 acres of seed plots annually.

In Arkansas, C. J. Nettles estimates that about 78 percent of hybrid seed corn sold in the state is produced by seven companies, including Funk, DeKalb, Pfister Associated Growers, Pioneer, Corneli, Dixie and McCurdy. All other sources account for approximately 22 percent of seed sales including about 20 commercial companies and from experiment station sources.

E. S. Horner estimated that Florida growers supply seed for about 100,000 acres out of 500,000 acres of corn grown in the state. Three companies, McNair Seed Co., Laurinburg, N. C., Greenwood Seed Co., Thomasville, Ga., and Cotton Producers Association, Atlanta, Ga., probably ship in to Florida and sell approximately 35,000 bushels of Dixie 18 each year. Funk's and Coker Pedigreed Seed Co., Hartsville, N. C., each sell approximately three thousand bushels of hybrid seed in Florida.

Use of Experiment Station Inbreds by Hybrid Seed Producers

A list was compiled by a subcommittee of the North Central Corn Breeding Technical Committee, with M. T. Jenkins, chairman, of inbred lines released by different states during the years 1946 to 1955 inclusive. Through the aid of William Heckendorn, questionnaires were sent to members of the hybrid seed corn trade. The replies received gave the number of bushels of double-crossed hybrid seed of the 1956 crop of which these lines were a parent.

Fifty-two seed producers replied from 12 different states. There were 17 replies from Illinois, seven from Indiana, six each from Iowa and Minnesota, five from Ohio, four from Missouri, two from Virginia, and one each from Wisconsin, Nebraska, New York, Texas, and Georgia. The total bushels of hybrid seed produced in 1956, of which inbreds released by the Experiment Stations during 1946 to 1955 were a parent, was 4,738,022.

It is evident from these data that inbreds released by Experiment Stations from their breeding programs have been of great importance to the hybrid seed industry. There is reason to conclude that the figure of over 4 million bushels as reported may overemphasize the use of these inbreds, as a double-cross hybrid from four station released inbreds would lead to four times as many bushels reported as were produced. However, inbreds released prior to 1946 without doubt are still in wide use by the seed trade. While 52 replies are sufficient to indicate the rather wide use of station released inbreds, there are many seed producers of hybrid seed from which replies were not obtained. The results of the questionnaire as summarized seem of general interest as a phase of the hybrid corn story.

Chapter 17 THE FOUNDATION SEED PROGRAM FOR OPEN-PEDIGREE HYBRIDS IN VARIOUS STATES

Delayed Release of Inbred Lines

The Directors of the Experiment Stations of the North Central Region at their 1941 November meeting adopted a policy for the delayed release of inbred lines from Experiment Station programs. This is expressed in the following motion,

> That the agricultural experiment stations of Ohio, Indiana, Illinois, Iowa, Missouri, South Dakota, Nebraska, Kansas, and any other of the North Central States as may from time to time wish to join this group, adopt a uniform policy of delayed release of inbred lines of corn developed at their respective stations, and those States adhering to the non-release policy will supply the above stations or their authorized agency inbred seed for the production of single crosses.

The purpose of the motion was to set up a plan of control of a new inbred by the Experiment Station during the early years of multiplication, before its full release to the public. The policy implies that each station must provide methods for growing, processing and storing limited amounts of foundation seed under careful control. Cooperation with other states, that were not using the principle of delayed release, was facilitated by agreements not to release an exchange line without complete approval by the station responsible for the production of an inbred.

At a later meeting there was a modification of the delayed release procedure to make it possible to release inbreds that excelled in special characteristics that would be of value to other station corn breeders or to breeders of closed pedigree hybrids. These inbreds would be released to the public whenever their characters had been established even though the in-

breds had not been proven of value for use in single- or double-cross hybrids. Such inbreds would be of value as a source of disease or insect resistance, chemical composition, male sterility or other characteristics.

Programs of Various States

A foundation seed program has been developed in each of the important corn producing states. In some cases, as in Wisconsin, Minnesota, Nebraska and Kansas, the foundation seed program is carried out as an Experiment Station activity. In other states, notably Illinois, Ohio, Michigan and New York, the increase and sale of foundation seed stocks of hybrid corn is carried out by a Cooperative Organization.

A brief outline of the procedure in each of the states includes an explanation of the overall plan of procedure, the type of organization, the relation to the Experiment Station program, and the method of release of inbred lines.

IOWA The Committee for Agricultural Development is a non-profit, non-stock organization responsible for the increase and distribution of valuable products developed by the Iowa State University and the Iowa Agricultural Experiment Station. A Board of Trustees elected from the membership directs the operations of the organization. The membership includes the President of Iowa State University, the Director of the Experiment Station, a member of the University staff as treasurer and business manager, a secretary from the Extension Service, seed growers and a County Extension representative.

Foundation seed of inbred lines of both dent and popcorn is produced and distributed by the Agronomy Department. The release policy followed is the one recommended by the North Central Corn Breeding Research Committee and approved by the Experiment Station Directors of the same region.

(Information furnished by production manager of the Committee, Charles D. Hutchcroft)

ILLINOIS The Illinois Seed Producers Association is a cooperative. Its membership includes most of the hybrid seedsmen in Illinois and a number of seedsmen interested in other crops. This association serves as agent of the Illinois Agricultural Experiment Station for the maintenance, increase, and distribution of seed and propagating materials of superior varieties, lines, and strains, and for the improvement of certain breeding materials.

The director of the Illinois Agricultural Experiment Station appoints an advisory committee to the Illinois Seed Producers Association. Members of this committee represent the various crops being improved by the station. The committee also includes the associate director of the station and the heads of departments concerned.

The principal functions of the advisory committee are:

1. To make recommendations to the Illinois Seed Producers Association concerning the crop varieties, lines, and strains to be maintained and increased.
2. To supervise the transfer of seed and propagating materials between the Illinois Agricultural Experiment Station or other sources and the Illinois Seed Producers Association.
3. To establish policies and standards for the production, processing and distribution of all seed and propagating materials being maintained or increased by the Illinois Seed Producers Association.
4. To approve and supervise the programs of breeding and varietal improvement carried on by the Illinois Seed Producers Association.

In return for services rendered by the Illinois Agricultural Experiment Station, the Illinois Seed Producers Association pays to the University of Illinois a fee based on the quantity of seed or propagating material sold during that fiscal year. These funds are used by the station in furtherance of its crop improvement program.

Inbred lines of corn developed by the University of Illinois may be released to the public when they have demonstrated superior combining ability for yield, standability, disease resistance, insect resistance, chemical composition, male sterility, or other characteristics. Such lines may form a part of a newly developed Illinois hybrid or be of potential value to other corn breeders. Inbred lines of corn developed by others will not be released without their approval. Hand-pollinated inbred seed of released lines are available in 100 kernel packets at $2.00 per packet.

(Information furnished by R. W. Jugenheimer)

INDIANA The Agricultural Alumni Seed Improvement Association, under control of a board composed of seed producers and members of the Purdue staff, is the foundation seed stock organization. This association, by contact with the Purdue Agricultural Experiment Station, increases inbred lines

and then produces single crosses for sale to seed producers. This association supplies seed stocks for both open and closed pedigree hybrids.

A new inbred line must prove its potential in hybrid combination (not necessarily a recommended hybrid) before it is eligible for general release. Essentially the "delayed release" program has been discontinued at Purdue.

Purdue recommended hybrids and closed pedigree hybrids tested by the Purdue Agricultural Experiment Station are eligible for Indiana certification.

(Information furnished by K. E. Beeson)

OHIO Foundation seed stocks are produced by the Ohio Hybrid Seed Corn Producers, Croton, Ohio. The producers of Station hybrids are members of this association. Members of the Agricultural Experiment Station act in an advisory capacity but with no official connection. The Seed Producers Association has a board of trustees, a paid manager and staff. Foundation seed stocks are produced on association land and under contract with member producers.

New Experiment Station inbreds are loaned to the association ahead of general release in order to build up seed stocks, in conformity with a "delayed release" program as is followed by many of the states in the North Central Region.

(Information furnished by G. H. Stringfield)

MICHIGAN Foundation seed of inbred lines and single crosses are produced by the Michigan Foundation Seed Association. Single-cross seed is sold to producers of certified seed (resident and non-resident) who agree to have the seed crop offered for certification. The Association by means of a memorandum of agreement with the Experiment Station is designated as the official agency for the production of all Foundation seed used in production of certified seed in Michigan. No member of the Station Staff is on the Board of Directors nor do members of the Staff take an active part in management, serving only in an advisory capacity. The manager of the Foundation Seed Association is an Association employee.

Inbred lines developed at the Michigan Station are released to private concerns three years after the hybrid has formally been released for seed certification in the state. This allows the certified seed producers three full years of seed production before the inbred lines are released to private agencies.

(Information furnished by E. C. Rossman)

WISCONSIN The College of Agriculture has maintained and increased the inbred lines involved in the Wisconsin corn hybrids since 1933. Foundation seed stocks are produced on a contract basis under the direct supervision of the College, which dries, processes, and distributes them to approved seed growers.

Official seed certification of hybrid field corn has been required by law in Wisconsin since 1941 and prior to that time, by Regulation of the Wisconsin Department of Agriculture. As carried out in Wisconsin, this has been a very satisfactory plan alike for seed producers and for the farmers who plant the seed. In recent years the Station has been providing pedigrees and foundation seed stocks to Wisconsin seed growers for the production of "closed" pedigree hybrids. These have been tested adequately to qualify for certification. Such pedigrees are not the same as for hybrids distributed under open pedigrees as Wisconsin hybrids.

In respect to the certification of the closed pedigree hybrids in Wisconsin, they can be rendered eligible by a minimum of two years official testing in Wisconsin, or by having been officially tested and approved for certification by any officially recognized testing agency in any other state.

The owner of a closed pedigree hybrid is also required to affirm that its basic pedigree is not the same as that of any open pedigree hybrid previously produced and distributed under a different variety designation.

Wisconsin has followed a policy of "delayed release" of inbreds since the spring of 1946. Germ plasm lots are made available to private individuals at the present price of $2.50 per lot.

(Information furnished by N. P. Neal)

MINNESOTA The Department of Agronomy and Plant Genetics of the Minnesota Agricultural Experiment Station, Institute of Agriculture, under Project 1313, has charge of the production and sale of seed of inbred lines of superior combining ability and the single-cross parents of superior open-pedigree hybrids developed by state or federal agricultural experiment stations. In general, the policies of increase and distribution of foundation seed corn are established by a Corn Committee made up of staff working on corn and, in addition, the director of the experiment station. The leader of the project has direct charge of all phases, although he has very competent associates in charge of individual phases.

Figure 29

Agronomy Seed Stocks Building at the right of the front steps and the Minnesota Crop Improvement Association Building at the left. The entrance to both buildings is from a central corridor. At the right of the Seed Stocks Building there are two special seed storage buildings. One of these is equipped for the control of temperatures and humidity.

The Seed Stocks Building was built with funds provided by sales of foundation seed. The office building and laboratories belonging to the Minnesota Crop Improvement Association are under the control of a board of directors of that Association. A part of the cost of this building was financed by Seed Stocks sales. (Courtesy Minnesota Agricultural Experiment Station)

The increase of seed of inbred lines is made at the Central Station at St. Paul and the Southern Experiment Station at Waseca. Nearly all of this increase is by hand-pollination, requiring approximately 25,000 hand pollinations per year. The project also has an overwinter testing program in Florida.

Single-cross seed is produced on the basis of requests made fourteen months in advance of planting. The single-cross plots are grown in cooperation with commercial seed producers and the branch stations, although all phases are under the immediate direction of Project 1313 personnel. As a rule, so far as is possible, sufficient seed of inbreds and single crosses are produced to have constantly available a supply of seed needed for a two-year period. Germination tests are made on inbred and single-cross seed both in the seed laboratory and in the cold test. The grower retains 40 percent of the single-cross seed he produces for his part of the contract.

In 1956, the Minnesota station initiated a new inbred line release policy whereby, "Inbred lines of corn developed by the University of Minnesota will be released to the public when they have been proven to be of superior combining ability for yield or other characters. Inbred lines developed by other states will not be released without their approval." At present, 100-200 kernels of a released line is sold at $3.00 per packet for regular fertile and $3.50 per packet for male sterile and for fertile non-restorer counterparts.

(Information furnished by Carl Borgeson)

NEBRASKA The Foundation Seed Division of the Agronomy Department is responsible for the production and sale of all foundation seed stocks after the initial seed supply has been released by the Agronomy Department for further increase for farmer's use. It operates through a Foundation Seed Manager who is a member of the University staff, a foreman, and such other assistants as are necessary. This Foundation Seed Division receives no appropriated funds except as certain facilities have been made available and as the administrative and business segments of the University are utilized. Otherwise it is self-supporting through the production and sale of foundation seed stocks. The Foundation Seed Division has the use of 1500 acres of land for seed stocks production in four localities, a good laboratory, processing facilities, storage buildings, and equipment at Genoa and Lincoln.

The Manager operates in accordance with rules and regulations developed by a Foundation Seed Committee whose per-

sonnel consists of the Dean of the College of Agriculture, the Director of the Agricultural Experiment Station, the Director of the Agricultural Extension Service, the Chairman of the Foundation Seed Committee who will be from the Department of Agronomy, the Foundation Seed Manager and provided the chairman of the Foundation Seed Committee is other than the Chairman of the Department of Agronomy, the Chairman of that Department.

There also is a Special Advisory Committee whose duties consist only of counseling and guidance, and is subject to the call of the Chairman of the Foundation Seed Committee who shall be the Chairman of the Committee. This Committee consists of the plant breeders and extension specialists of the Agronomy Department, officials of various designated agricultural organizations, and a certified seed grower chosen by other members of this committee.

The policy for release of inbred lines follows the recommended plan adopted by the Directors Conference of the North Central States.

The seed certification program, which is carried out in close collaboration with the Agronomy Department, is handled by the Nebraska Crop Improvement Assocation. It operates through a salaried manager and laboratory staff who are officed on the Agricultural College Campus. The certification program is financed by specific fees levied on the individual growers of certified seed, on a unit basis.

(Information furnished by T. A. Kiesselbach)

KANSAS Foundation seed of inbred lines and single crosses of Station hybrids is increased and made available to producers by the Agronomy Department of the Agricultural Experiment Station.

Foundation seedstocks are produced in part in cooperation with seed producers. It is not a Station requirement that seed of Station double crosses be certified.

Inbred lines are eligible for release to private growers when used in a hybrid that is approved by any State Experiment Station for commercial production. Lines of special breeding value are eligible for release at any time after possession of the unique characteristic has been established.

(Information furnished by William R. Findley)

NORTH DAKOTA Foundation seed stocks of inbred lines are produced by the Agricultural Experiment Station. Foundation seed stocks of single crosses of Station recommended hy-

brids are produced by the Experiment Station and cooperating seed growers on a share basis for distribution to growers of commercial seed. Since 1945 inbred lines of Station hybrids have been released so that interested seed growers may increase their own seed stocks when they desire to do so.

(Information furnished by William Wiidakas)

SOUTH DAKOTA The Foundation Seed Stocks Division of the South Dakota State College increases inbred lines and produces single crosses of Station recommended hybrids for sale to South Dakota seed growers. The single crosses may include also hybrid combinations originally produced, or recommended, by other State Experiment Stations. The seed grower of such hybrids agrees to apply for seed certification. Inbred lines of recommended hybrids are released on the "delayed release" policy now followed by many Stations of the North Central Region.

(Information furnished by V. A. Dirks)

MISSOURI The Missouri Seed Improvement Association is responsible for producing and maintaining inbred lines and single crosses of Station hybrids recommended for Missouri. It also is the official agency for the certification of corn hybrids. This Association is under the control of a seven-man board of directors, elected by the membership and including the Dean of the College and the State Commissioner of Agriculture.

The offices and warehouse of this Association are on Station grounds. There is no requirement that Station produced and recommended hybrids be certified.

Inbred lines are released if they have proven merit, including one or more of the following: high combining ability, lodging resistance, drought resistance, and resistances to disease or insect pests.

(Information furnished by C. O. Grogan)

KENTUCKY Foundation seed, of inbred lines and of single crosses, is produced by Kentucky Seed Stocks, Inc. Seed of inbred lines used by this organization is obtained from the corn breeding program of the Kentucky Agricultural Experiment Station, and is produced under the direction of the corn breeder by continuous selfing in ear-row progenies. The breeder determines what inspections of single-cross seed production are made, and after inspection the Manager of Seed Stocks, Inc. attaches the appropriate tag to the seed.

The Director of the Experiment Station has designated Kentucky Seed Stocks, Inc. as an agency for producing Founda-

tion seed. The board of directors is composed of seed producers; however, the salary of the secretary-manager, in recent years, has been paid from Station funds.

(Information furnished by F. A. Loeffel)

TENNESSEE Foundation seed stocks are produced under the direction of the Tennessee Seed Producers, Incorporated with headquarters at Nashville. In cooperation with the University of Tennessee and the United States Department of Agriculture foundation seed stocks are produced, particularly by contracting with producers and institutions.

(Information furnished by L. M. Josephson)

WEST VIRGINIA Foundation seed stocks of inbreds and single crosses used in hybrids released by the Agricultural Experiment Station are maintained by the Agronomy and Genetics Department of the University Experiment Station.

(Information furnished by M. W. Johnson)

NEW YORK The New York Foundation Seed Stocks Cooperative, Inc., through agreement with the New York Agricultural Experiment Stations, has a monopoly on the multiplication and distribution of Foundation Seed of hybrid corn of Experiment Station hybrids. The Board of Directors of the Cooperative and a Station Seed Stocks Committee decide jointly regarding the materials to be increased. The increase of seed stocks by the Cooperative is arranged in cooperation with the plant breeder and the Stations Seed Committee. The plant breeder furnishes Breeders Seed to the Cooperative and gives other advice as needed.

The New York Agricultural Experiment Stations follow the policy of "delayed release" of inbreds.

(Information furnished by H. L. Everett and A. A. Johnson)

PENNSYLVANIA Prior to 1954 the College of Agriculture operated a foundation seed service for growers of certified seed. The Pennsylvania Foundation Seed Cooperative was organized in 1954-55 for the purpose of meeting seed requirements of growers of certified seed of hybrid corn and small grains. The Board of Directors includes representatives of seed growers, farm cooperatives and commercial seedsmen. There are also representatives of the Experiment Station, Extension Service and State Department of Agriculture who serve Ex-Officio, to insure that all operations are genuinely in the public interest.

Inbred lines originating from the Pennsylvania Station program are handled on a three year delayed release plan, with the

Pennsylvania Foundation Seed Cooperative as the sole agent for the production and distribution of single crosses involving such new lines, during the three year period.

(Information furnished by H. B. Sprague)

NORTH CAROLINA Foundation Seed stocks of inbred lines are increased by the North Carolina Foundation Seed Producers, Inc., and this Cooperative increases for sale all foundation single-cross seed for certification purposes. This Cooperative is a non-profit group of farmers and seed producers which maintains an office and warehouse for the distribution of foundation seed. The procedures are arranged through a memorandum of agreement between the Experiment Station and the Board of Trustees of the Foundation Seed Producers. Title to all unreleased strains of any crop which is being increased by the Foundation remains the property of the Station until such strain is formally released by the Station. Seed of Station hybrids is offered for certification by the North Carolina Crop Improvement Association.

An inbred line may be released to the public when its value has been definitely established in a corn hybrid recommended for commercial production, and when its suitability for commercial production has been determined by limited seed production under typical field conditions for not less than three years.

Some inbred lines possess unique characteristics of special breeding value such as disease resistance, insect resistance, chemical composition, sterile cytoplasm and fertility restorers, but are not likely to be used in a commercial hybrid because of poor combining ability or other weaknesses. Such inbred lines may be released to the public at any time for their special breeding value.

An inbred line must meet the approval of the experiment station release policies in the same manner as a variety of a self-pollinated crop.

At the time of release of a new inbred line an appropriate experiment station announcement, including a description of the inbred, shall be made. The experiment station shall specify the terms of the release, including amount of seed, unit cost and other details.

(Information furnished by Paul H. Harvey)

SOUTH CAROLINA The South Carolina Foundation Seed Association, a non-profit organization, is responsible to a Board of Directors elected from the members and to the Director of the Experiment Station. This association handles the in-

crease and sale of Foundation seed of inbred lines and of single crosses of recommended Experiment Station hybrids.

To date no policy has been established concerning the release of inbred lines produced by South Carolina. The program is relatively young and no hybrids have been put in production thus far. It is expected that some sort of delayed release policy will eventually be adopted.

It is required that Station recommended hybrids be certified if produced by foundation seed obtained from the Seed Association.

(Information furnished by Alfred Manwiller)

VIRGINIA The Virginia Crop Improvement Association, Inc., is a non-stock, non-profit, educational organization. It has an agreement with the director of the experiment station in which the association received breeder seed from the experiment station. From this seed the association multiplies foundation seed. This seed is under the control of the experiment station until it is released. The expense of multiplication is borne by the association. The policy of delayed release of inbreds is followed by the Virginia Agricultural Experiment Station.

(Information furnished by C. F. Genter)

GEORGIA A foundation seeds organization, Foundation Seeds, Inc., was established in 1958 to work in cooperation with the Georgia Crop Improvement Association (established in 1946). The organization has charge of the increase of Foundation Seed stocks of inbred lines and single crosses of Station hybrids recommended for Georgia. Single-cross seed of hybrids from states other than Georgia are obtained from out-of-state sources. Information to those growers interested in such foundation seed stocks is available by Foundation Seeds, Inc. on request. The work of this cooperative is carried out in close collaboration with the Agricultural Extension Service. All hybrids certified by the Georgia Crop Improvement Association must be recommended by the Extension Service based on a minimum of three years trials by the Georgia Experiment Stations. The College of Agriculture discourages the production of Station recommended hybrids without certification. The Georgia Stations follow a policy of delayed release of inbreds.

(Information furnished by A. A. Fleming)

FLORIDA The Experiment Station produces seed of inbred lines and makes this seed available to the Florida Foundation Seed Producers, Inc., which contracts with individual grow-

ers for the production of single crosses. Close cooperation exists between the two organizations.

A delayed release policy is followed with inbred lines. Usually they are released after successful performance. The trial period required is left largely to the discretion of the breeder.

Station hybrids for which foundation seed is made available must be certified, and certification procedures are carried out by the State Department of Agriculture.

(Information furnished by E. S. Horner)

MISSISSIPPI The Mississippi Agricultural Experiment Station receives a state appropriation for the production of hybrid corn seed stocks. Increase fields of inbreds and single crossing blocks are under the direction of an experiment station employee and seed is processed and stored in station facilities.

(Information furnished by Robert C. Eckhardt)

TEXAS The Foundation seed program is handled by the Experiment Station as a unit in the Department of Agronomy. A Foundation Seed Stocks Building at College Station is adequately equipped for processing and storage of Foundation seed stocks. At present an Extension - Experiment Station employee, with adequate staff, has charge of the production and distribution of foundation seeds. Single crosses of Experiment Station hybrids are produced in the Foundation Seed program of the Agricultural Experiment Station. Inbred lines are released to growers interested in propagating them.

(Information furnished by J. S. Rogers)

OKLAHOMA The Oklahoma Crop Improvement Association is the organization designated by the Experiment Station for the production and sale of Experiment Station recommended hybrids.

The Oklahoma Seed Stocks, Inc. is charged with increasing breeders seed and producing foundation seed. It is the joint function of the Experiment Station and the Extension Division. The Oklahoma Crop Improvement Association is the organization in charge of seed certification.

(Information furnished by J. S. Brooks)

COLORADO Foundation seed stocks of recommended Station hybrids are increased for sale by the Foundation Seed Project of the Agronomy Section, Agricultural Experiment Station. Such seed stocks are grown on the Station Agronomy Farm or in cooperation with seed growers. In all cases the increases

are under the careful supervision of Station personnel. The project, as described, deals only with increases of inbred lines and single crosses of Station recommended hybrids. Inbred lines are released to other experiment stations when requested. They are released to growers, hybrid seed companies, or the public only when they appear in a recommended hybrid grown in Colorado. Seed certification of double crosses is under the State Board of Agriculture; however, its authority for hybrid corn has been delegated to the Extension Service which was responsible for establishing the Seed Certification Service to handle certification problems.

(Information furnished by Warren H. Leonard)

ARKANSAS Corn hybrids tested in 1931, 1932 and 1938 from other states were unsatisfactory. The first successful hybrids were grown in 1939. No hybrid as yet has been bred and released by the Arkansas Station.

(Information furnished by D. A. Hinkle)

CALIFORNIA No hybrids by the California Stations have been released for distribution. One company is growing seed of open-pedigree lines and hybrids from another state.

(Information furnished by D. G. Smeltzer)

Previous discussion, regarding the foundation seed program for open-pedigree hybrids, has referred to procedures in use to make inbred and single-cross seed available from research programs carried out in relation to breeding researches conducted by State Agricultural Experiment Station workers or by members of the United States Department of Agriculture. In each case the name of the individual who furnished the information has been included and the descriptions as given were approved by the men referred to in each case.

It has been called to my attention recently that some private companies produce and sell foundation seed of open-pedigree inbreds and single crosses. The writer has not attempted a complete survey of these companies. Companies mentioned by my informant as important producers of foundation single crosses were Clyde Black and Son, Ames, Iowa; Holden Foundation Farms, Williamsburg, Iowa; Bear Hybrid Corn Company, Decatur, Illinois, and C. E. Troyer, La Fountaine, Indiana.

Chapter 18 WHAT OF THE FUTURE

Introduction

The history of hybrid corn as written has emphasized the many phases of both basic and applied researches that were an essential part of its development. The work of individual investigators, who played an essential part in the development of special phases of basic research and breeding applications, has been reviewed. Many other workers not mentioned also have aided in the development of hybrid corn.

Basic research in corn genetics and cytogenetics has been reviewed rather briefly, although it is appreciated that these phases of research are an essential part of the story. The development of methods of breeding corn has been reviewed in greater detail than has been attempted for basic genetical studies, although it seems evident that plant breeding methodologies are based upon genetical principles. Thus, Theodosius Dobzhansky has written, as have several others, - "Hybrid corn remains, to date, the most practical attainment of genetics."

Special mention may be made that the early studies of breeding and genetics of the present century, of essential importance in relation to hybrid corn, were made outside the Corn Belt. These include the work of Shull at Cold Spring Harbor from 1905 to 1914, inclusive, which has been reviewed in detail, and that of East and others at the Connecticut Agricultural Experiment Station from 1905 to 1909, and subsequently at the Bussey Institution of Applied Biology at Harvard University. East continued to direct the plant breeding and genetical studies at the Agricultural Experiment Station through 1911, and advised regarding the continuation of these studies through about

1920. Even after 1920 East played an important role in the New Haven researches, as various research workers on the Experiment Station staff used thesis problems, carried out as Station research, of which East was the adviser. These research studies at the Connecticut Agricultural Experiment Station were supported largely by Adams Funds for basic research.

The review of Conway Zirkle of biological research on inbreeding and outbreeding prior to the present century made evident that most of the principles relating to the effects of inbreeding and outbreeding had been discovered prior to the studies of East and Shull. It is evident, however, that these principles were not generally understood by many students of biology. Therefore it has been concluded that without the early studies of Shull and East and coworkers in the present century the development of hybrid corn would have been long delayed.

The developments in genetical and breeding principles relating to hybrid corn have been reviewed in considerable detail. Important phases of these studies may be summarized here, although further researches are being made in many of these phases today. They include, -

1. Basic knowledge of the genetics and cytogenetics of corn, with special reference to individual characters. Through special technics, genetic and cytogenetic methodologies have been developed, that aid in the determination of the number, nature, and location in the chromosomes of genes responsible for the inheritance of characters, including resistances to plant pests and in relation to the inheritance of combining ability.
2. Basic knowledge of corn breeding methodologies with particular relation to corn genetics principles. These may be briefly mentioned.
   a. The causes of heterosis including the dominance of, or partial dominance of, linked growth factors, the interaction of alleles at a single locus called, by some researchers, heterotic loci, and the interaction of alleles at different loci referred to in some cases as epistasis.
   b. The double-cross method of seed production, that made hybrid seed corn production feasible.
   c. The rather definite relation between the performance of inbreds, as inbreds, and their combining ability in crosses. Although any one inbred character, such as ability to withstand lodging, has only a low correlation with combining ability in crosses, there is a positive

and important correlation between the combined rating of inbred lines for many growth characters and the performance in their crosses, with particular reference to yield of grain and time of maturity.

d. The knowledge that some inbred lines have the ability to combine well with most other unrelated inbred lines, that other inbreds combine well in some similar crosses, but not in others, and that still other inbreds are, in general, low combiners.

e. The prediction of the general combining ability of homozygous and heterozygous selections by crosses with a tester, or testers, that are heterogeneous and heterozygous, and that are not, as a rule, related to the inbred lines.

f. The performance of double crosses, i.e. the double cross, (A x B)(C x D), can be predicted with great accuracy from the average of the single crosses, A x C, A x D, B x C, and B x D. This prediction method has been used largely in relation to yield and time of maturity. To determine relative time of maturity moisture percentage of grain at husking has been used.

g. The specific combining ability of an inbred with other unrelated inbreds, is correlated to some extent with the rating for general combining ability of the inbred under test when selected unrelated inbreds are used in the study. For example, in a series of diallel crosses of inbreds with other inbreds, general combining ability can be estimated rather accurately from the average of all single crosses for each inbred. The higher yielding single crosses usually are obtained from single crosses where one or more of the parent inbreds have been rated previously as high in general combining ability. Specific combining ability of an inbred, in comparison with other inbreds, can be estimated by comparing the extent of deviations of individual crosses of that inbred with the average of all of its single crosses. There often are wide deviations in performance of an inbred in single crosses with the other inbreds.

h. Genetic diversity has an important relation to both general and specific combining ability. Thus for equally desirable inbreds greater heterosis often results from crossing inbreds that are more widely unrelated. For example, most commercially important double crosses

have resulted from crosses of inbreds from diverse sources. As a general rule, it has proven difficult to obtain desirable double crosses by using inbreds derived from a single variety.

i. The only method of knowing, very exactly, how two or more inbreds will combine with each other is by actual test.

j. Inbreds can be improved, as inbreds, and for use as parents in crosses, by definite breeding methods. The method used will depend somewhat on the nature of the character and in many cases it may be desirable to incorporate genes controlling character reactions, such as resistance to plant pests, into all inbred lines used in the particular cross, or crosses, to be made.

Within the text of the hybrid corn story, breeding procedures have been outlined. Those specifically featured include the pedigree method, back crossing, convergent improvement, multiple convergence, early testing, gamete selection, and reciprocal recurrent selection.

Major developments in hybrid corn history include the organization of cooperation on an informal basis first by Richey and others, and later placed on a more formal basis by the Directors of the North Central Experiment Station group in 1925. Similar cooperation was developed later for the Southern and North Eastern Experiment Stations. Interchange of material and ideas of research workers, not only in various regions in the United States but throughout the world, has been in a large measure responsible for the success of the hybrid corn program.

Other important phases that have greatly aided in hybrid corn production include the developments by commercial seed companies and by experiment station workers of all phases of hybrid seed production, seed processing, and seed treatment in such a manner that seed of high quality of adapted hybrids is generally available to the grower.

These more important developments together with others of a somewhat similar nature furnish the background for a brief discussion of future possibilities in hybrid corn improvement. These may be discussed under a few general headings and will include those that appear, to the writer, of greatest promise.

Resistances to Plant Pests and to Special Conditions of the Environment

There have been many discoveries of resistances to important diseases and insect pests. In many cases there seems to be an excellent opportunity to develop and utilize these types of resistance to a much wider degree than has yet been accomplished.

Many inbred lines and hybrids have been developed that are more resistant to smut than normal open-pollinated varieties. The extreme resistance of certain inbreds, such as that reported by Burnham and Cartledge (1939), has not as yet been added to the germ plasm of inbreds now in use in the hybrid corn program. Here is an important future possibility.

Great progress has been made in developing inbreds that are resistant to the organisms responsible for ear and stalk rots. This information has been developed largely though the cooperative attack of plant pathologists and plant breeders on these problems, using controlled inoculation methods. However, the number of organisms that are responsible for root and stalk rots are rather large, and the opportunities for developing hybrids that are more resistant to these diseases seem very great. The wider use and value of ear and stalk rot resistances necessitate much further research.

Leaf blights in some areas are a constant menace. *Helminthosporium turcicum* is a serious foliage disease of corn in some sections of the United States. Resistance is available and transmissible. Much further work is needed to solve the problem of controlling this and other leaf foliage diseases.

Basic studies of the nature of disease resistance have been carried out by a few investigators. In most cases little is known about the causes. A recent summary of the studies at Purdue is cooperation between Dr. J. Kuc of the Department of Biochemistry and Dr. A. J. Ullstrup of the Department of Botany and Plant Pathology have been furnished the writer by Dr. Ullstrup. The results of this study are summarized here in a quoted abstract by Dr. Ullstrup of a short talk given at the North Central Corn Conference in Chicago in 1958.

"In a study of the nature of resistance in corn to Helminthosporium leaf spot (incited by *Helminthosporium carbonum* Race I) it has been found that an extract prepared with ethanol from heavily inoculated resistant seedling leaves is completely

inhibitory to germination and growth of parasite *in vitro*. Similarly prepared extracts from inoculated, susceptible host material are only slightly inhibitory. Extracts prepared from non-inoculated resistant or susceptible host tissue, on the other hand, support good growth of the fungus. Assay for activity of extracts is made by combining the dry residue of the latter with potato-dextrose agar.

"When the toxic extract from inoculated resistant host tissue is partitioned into ether and water fractions, both fractions support good growth. When the two fractions are combined, however, toxicity is again restored and is equivalent to that of the original crude extract.

"Drying of the inoculated, resistant seedling leaves for more than 4 hours at 72° F. destroys the toxic material that appears to be formed in the resistant host cells in response to penetration by the parasite.

"Thus far neither chromatographic nor spectrophotometric analysis have given any clue as to the nature of the toxic material in extracts prepared from inoculated resistant host tissue. The toxic material is stable to autoclaving and is active against a number of fungi other than *H. carbonum*."

In recent years double-cross hybrids have been developed at Ohio, Minnesota, and in other states, that are resistant to early attack of first brood corn borers. While there is some evidence that leads to the conclusion that there also are wide differences in tolerance among inbreds to the attack of second and later broods, this phase of work has not been widely developed and the value and utilization of resistance to first brood borer attack necessitates further intensive study.

The importance of resistance to the corn ear-worm is appreciated. Many inbreds and hybrids now available have little or no inherited resistance to the ear-worm. Further studies are needed. Resistances to attacks of grasshopper, white grubs, rootworms, aphids and chinch bugs, while known in each case, have not been utilized to as great extent as can be accomplished.

Throughout the story agronomic characters, such as yield, have been referred to as characters dependent upon the interaction of genes. It is evident that yield, as a character, is modified in expression to a much greater extent by environmental conditions than such qualitative characters as color of flower or seed. These color characters, in some cases, also may be modified in expression by extremes in environmental conditions. What is inherited for all characters is the manner

of reaction under the particular set of environmental conditions. This is a basic and essential viewpoint, and these relationships are emphasized as a phase of viewpoint by many, if not all, teachers of Plant Breeding.

In relation to the hybrid corn story much has been learned regarding such characters as yield as modified in expression by environmental conditions, and the results of this knowledge have been of great importance in corn production. For example, new knowledge of selective herbicides, modifications in cultural practices, responses to rates of fertilization and increases in rates of stand have led in many cases to marked increases in yield.

Some inbred lines and their hybrids respond in a more favorable way, than other inbreds, to heavier rates of planting. Thus inbreds and their hybrids may be classified in relation to their response to crowding as sensitive, and thus not capable of increasing yield under heavier rates of planting, and less sensitive lines that respond in a more favorable way to planting under heavier rates. In many cases, the necessary researches in relation to important inbreds and their hybrids have not been made, although the preliminary studies have indicated rather clearly the value of more extensive knowledge.

Today and in future years much more research is needed to determine breeding procedures with particular relationship to environmental conditions as modified by shade, nutrients, clouds, sun, parasites, or culture. Although extensive preliminary studies have been made under conditions of partial control in the field to shading, carbon dioxide content of the air as modified by heavy rates of planting, and wind currents, etc., the opportunities of future studies of yield components under various environmental conditions seem of basic importance. With the development of more complete control of growing conditions in research laboratories as have been available at Purdue University and elsewhere and have recently become available in the new Crop Research Laboratories at Minnesota, for example, it seems evident that many more researches, not only by the corn breeder, but for other crops, will be of essential importance in relation, not only to crop improvement, but also will lead to many physiological researches of basic importance to other fields of crop research. In the near future these essential studies will furnish information that will greatly expand the hybrid corn story, and other similar stories in crop improvement and crop research.

Development of Hybrids for Special Purposes

Double-cross hybrids have been produced, that are homozygous for the waxy gene, that have been used industrially in supplying a substitute for tapioca. The single-cross sweet corn hybrids now available excel in tenderness of pericarp and in qualities that are of special value for freezing and canning. These are valuable contributions.

It is well known from extensive studies that hybrid corn has a lower total protein percentage than comparable open-pollinated varieties. Ackerson and others (1946) have studied the utilization of open-pollinated and hybrid corn in an otherwise complete ration for growing chicks. The lot fed with the open-pollinated corn ration had a higher growth rate at the end of a six-weeks feeding trial than the lot fed with hybrid corn.

Dr. Robert Koch, Head of the Nebraska Animal Husbandry department states, "Various hybrids differing in protein content have been compared in livestock feeding tests, and no striking effects were noted."[1] Sprague, however, has suggested that selection for high-oil content leads automatically to increase in the balanced protein tryptophan. Added breeding and feeding studies are needed to determine the extent to which it may be possible to increase tryptophan content, and obtain hybrids which excel both in protein content and in feeding value as compared with hybrids now available, and at the same time maintaining adequately high grain yield.

There is available evidence regarding the inheritance of protein, zein, tryptophan, valine, leucine and isoleucine (see Hayes *et al,* 1955). Hybrids could be produced if that was desirable that would excel, over hybrids now available, in various chemical characters. Studies by Richey and Dawson (1948) on niacin content, which is of importance in relation to certain malnutrition disturbances in animals, gave data leading to the conclusion that inbreds and hybrids with high niacin content could be developed by selection for niacin content. Such selection did not appear to modify other agronomic characters.

High amylose corn has been grown under contract for industrial purposes. Kramer *et al* (1958a, b) presented data on the genetics of high amylose corn. The action and interaction of 5 genes, *ae*, *du*, su_1, su_2, and *wx* were found to condition

[1]Personal corespondence with Dr. T. A. Kiesselbach

amylose percentages in starch ranging from 0 to 70 per cent. The homzygous recessive for *ae* increased amylose content in the presence of the dominant condition of other genes mentioned from 27 per cent in normal seeds to 61 per cent. When *wx* was homozygous no amylose was produced, except in the presence of homozygous *ae* when amylose content was from 13 to 15 per cent. Thus, *wx* in the absence of *ae* was completely epistatic to the effects of other genes mentioned. Various combinations of *du*, su_1, su_2, when recessive, were partially epistatic to the effects of recessive *ae*. The *ae* gene was originally reported and named amylose extender *(ae)* by R. P. Bear (see Maize Genetics Coop. Newsletter in 1952).

Sandstedt *et al* (1962) have shown that, "a high amylose corn having a starch highly resistant to enzyme action proved to be highly resistant to digestion when fed to rats and chicks confirming the *in vitro* laboratory digestions." Ackerson (1961) previously found that, "starch from a high amylose type corn is used by chicks to a much lesser extent than starch from hybrid corn." Sandstedt *et al* have pointed out that such indigestibility could be important, since if high amylose corn were produced in excess of industrial needs, such material would be utilized in feed channels.

These reviews emphasize some of the problems faced in breeding high-amylose corn for industrial uses. It would not seem too difficult to produce corn that was higher in amylose content than that of normal hybrids based on present knowledge of the inheritance of amylose content; however, further study is needed to obtain as high content as possible in combination with high yielding ability and desirable agronomic characters. Similar problems without doubt will appear constantly in future breeding studies.

Breeding for Agronomic Characters

The wide use of Wf9 as one inbred of a single cross used as the female of recommended double crosses is rather clear proof that many double crosses now grown are not as desirable from the standpoint of high quality seed as others. This inbred appears to be very desirable in relation to seed quality. Many double crosses could be improved greatly in seed quality.

Promising results have been obtained at Illinois by E. R. Leng by incorporating the single recessive genetic factor

brachytic 2 into desirable standard inbred lines and their double-cross hybrids. The internodes of the dwarfs are much shorter than those of normal plants which results in hybrids about four feet in height. Under very favorable conditions, reconstituted double-cross dwarf hybrids have yielded somewhat less than the normal double crosses of similar genotypic constitution. The great value of dwarf hybrids is that they stand up much better than their normal corn hybrid counterparts. It seems probable that better dwarf double crosses than those now available will be developed by a somewhat broader system of breeding than the addition directly of the dwarf factor by backcrossing to available double crosses.

While one of the more important characters of double crosses, in comparison with normal corn, is their great ability to withstand lodging, it is appreciated by all corn breeders that some inbreds have much greater ability to transmit resistance to lodging than others. The improving of lodging resistance of the inbreds that are used in recommended hybrids, with particular attention to those which lack standing ability, would seem a valuable means of developing standard type plant hybrids that excel double crosses now available.

Some double crosses have the ability to continue to show an increase yield to a greater extent under heavy stands than others. Inbreds also differ in this characteristic and there is considerable evidence that this characteristic of inbreds is transmissible. There is excellent opportunity of developing double crosses that excel in this character. In recent years some studies have been made in relation to this problem, however, the extent of information is not very great.

Cytoplasmic sterility, in the presence of recessive nuclear factors for male sterility, leads to the production of male sterile offspring when an inbred carrying the cytoplasmic factor is used as a female of a single cross. There also are restorer genes that when introduced into a cross from the male parent lead to the production of male-fertility in the cross even though the female parent carries this cytoplasmic factor. In this case, as in many of a similar nature, there is a need for increased knowledge of the relation between the cytoplasmic factor and other agronomic characters including yield.

An interesting development is the marked trend toward the commercial production of single crosses. It is evident from the previous reviews that the best single cross can be expected to yield better than the best 3-way or double cross as developed

from any comparable stage in the breeding process. For the single cross only two inbred parent lines are used, while three inbreds are used in the 3-way and four in the double cross. Therefore it is less difficult to obtain a single cross, that excels in agronomic or quality characteristics, than an equally desirable 3-way or double cross.

The utilization of single crosses for the commerical crop has been dependent upon the production of inbred lines that in themselves are more vigorous than those previously available and that produce desirable seed. Although the cost of seed to the grower is as a rule higher for single than for double crosses, commercial growers of corn for grain seem to be willing to buy single-cross seed and pay the extra cost.

Such single-cross seed has been used extensively for many years for both sweet and pop corn where uniformity is a valuable asset. It will be of interest to note whether the reduced inherited variability in single crosses from plant to plant, as compared with double crosses, will lead to any great hazard for commercial producers of hybrid corn.

Other ideas of a similar nature could be presented. It seems probable to the writer that all crosses now grown could be improved in one or more agronomic characters. This statement is based on the common knowledge that some inbreds in each cross excel others in their ability to transmit desirable agronomic traits to their hybrid progeny.

Breeding for Higher Yield Performance

Much has been learned regarding general and specific combining ability, and of genetic diversity, in relation to breeding for higher yield. It is also appreciated that higher yield is only possible if environmental conditions are favorable. High yields require heavier, balanced conditions of fertility. There is constant need of more basic information.

The more recently introduced method of reciprocal recurrent selection appears, to the writer, to deserve more intensive utilization in future breeding programs. It may be suggested that original sources of material for this purpose could be synthesized from available known sources. To illustrate what is meant the writer suggests such material could be synthesized from present day breeding programs. From such material, as available for the single crosses discussed, where all possible

single cross combinations from 15 inbreds have been studied in yield trials (see chapter 8), it is suggested that several inbreds be selected that each appears to excel in all crosses with another group of several inbreds. The two synthetics produced from intercrosses within each of the two groups would seem excellent genetic sources for use in reciprocal recurrent selection. Desirable exotic germ plasm could be incorporated also into each of the groups using two unrelated sources, one for each group. Osler and Wellhausen[1] presented results that they interpreted on the basis that there were several unrelated open-pollinated corn varieties in Mexico that carried genes for high combining ability. They suggested also that these might be valuable sources for a new series of genes for high combining ability that have not yet been utilized by United States corn breeders.

It is hoped that these suggestions may lead to similar plans with different material that may help to determine the relative value of recurrent selection that could be studied in comparison with other methods of breeding. Studies of this nature would seem to have a wide application to the breeding of forage crops, particularly those with high self-sterility, where it would seem that reciprocal recurrent selection and the eventual use of single-cross hybrids appear to be of great economic value as a means of increasing yield performance.

The Genetical Basis of Heterosis

Although much has been learned regarding the genetical explanation of heterosis several leaders believe that until this problem has been analyzed more completely it will not be possible to obtain complete utilization of heterosis in corn breeding and also in other crop plants and in animal breeding.

Thus Hazel (1961) refers to Davenport (1908) as one of the earliest to point out "the implication of dominant gene action in causing heterosis." Hazel also refers to Crow (1952) who states "that the dominance hypothesis seems inadequate to explain more than an advantage of 1 to 5 percent in crosses as compared with parental stocks." Crow (1952) also writes, "It is clear that the dominance hypothesis is adequate to explain the deterioration

[1]Osler, R. D. and Wellhausen, E. J. Agronomy Abstracts, Nov. 1957, page 57.

that results from inbreeding and the recovery of vigor on outcrossing, but it is difficult to explain how hybrids could greatly exceed in fitness the equilibrium populations from which their parents were derived."

Burton and Sprague (1961) write, "Certainly, the ultimate extent and efficiency of hybrid use will depend upon a more adequate understanding of the phenomenon of heterosis and related problems in statistical genetics." They further list the following areas in need of future research, including the relative importance of various types of gene action, the magnitude of the genotypic environment interaction in relation to estimates of the several components of genetic variance and the nature of genetic differences between varieties.

And to show the differences in viewpoint regarding the genetical bases of heterosis one may refer to King (1961), who discussed, "Inbreeding, Heterosis and Information." He emphasized differences in randomly bred and inbred populations of drosophila with respect to the ratio of hatched eggs to total. In randomly bred populations the ratio is high while in inbred populations the situation is reversed and the ratio is low. Here apparently as in corn, while inbreeding leads to homozygosis, inbreds are more susceptible to environmental effects and less stable in their reactions. A careful reading of the paper leads to the conclusion that King considers that recent studies in biochemical genetics may lead eventually to a rather different explanation of heterosis, and perhaps regarding the inheritance of other characters, than the present day viewpoint that accepts the explanations based on what may be called classical genetics.

These references are sufficient to emphasize that more study of the genetical basis of heterosis is of great importance. The writer agrees that further studies of basic principles are essential, however, it seems that with present day genetical explanations of heterosis, there are almost unlimited opportunities for greater utilization of heterosis by the corn breeder.

Although mentioned previously it seems of value here to again emphasize the importance of more complete and adequate studies of the role of specific substances in heterosis as discussed by Whaley (1952) and Robbins (1952). In this connection a brief quotation from Robbins will serve to emphasize the importance of further researches. He writes,

> "It may be important to devote attention to the question of what the internal factors are which limit growth, what they are in inbreds, and how they are removed in heterotic hybrids.

We should consider in such investigations the role of essential metabolites, of growth inhibitors, and of other specific chemical compounds which materially modify growth. Microorganisms might be utilized as tools for the detection of growth stimulators or growth inhibitors."

Other Research Possibilities

The writer obtained suggestions regarding future hybrid corn studies from several research workers. Several suggestions seem of special interest.

In order that these excerpts regarding the viewpoints of some leaders in corn breeding are not misunderstood by the reader, it seems advisable to explain the writer's intention. Perhaps this can be done to the greatest advantage by reference to the quoted statements from G. H. Stringfield. He has been one of the leaders in the development of corn breeding who has continued to have the respect of all corn breeders with whom he has been associated. The few quotations from Stringfield, somewhat out of context, would give a very misleading view of his ideas of corn breeding unless it is understood that these discussions of "Other Research Possibilities" have been given to emphasize distinct phases of possible future work.

Dr. T. A. Kiesselbach who for many years in Nebraska was the leader in corn breeding and other agronomic studies has furnished the following statement,

"With respect to comparative field-plot tests for performance it is essential to use thorogoing plot-technic designed to provide adequate populations and randomized replication, comparable stands and border competition, uniform field treatment, with yields based on actual shelling percentage and comparable moisture content. Furthermore there should be caution in the use as improvement "measuring sticks" open-pollinated varieties that have been maintained for several generations by limited hand-pollination. Their yield may have deteriorated through loss of heterogeneity. A better measure would be some standard hybrid whose basic lines have been continued throughout in a homozygous state. For the establishment of general principles, especially accurate technic is desirable. In conjunction with statistical analysis of experimental data, it is important that the data

have been derived by sound plot technic, free from systematic errors."

In relation to the effects of Xenia which have been studied by Kiesselbach and co-workers the following quotation from personal correspondence with Dr. Kiesselbach seems of special interest.

"It seems worth while to study a large number of hybrids with special reference to Xenia effects upon the hybrid vigor of the kernels, and upon the percentage of water-soluble carbohydrate content in their endosperms. It seems possible that some hybrids with recessive factors for kernel size, weight and composition may give increased yields over the expected as a result of off-pollination, which does not occur in commercial fields planted to individual hybrids. In connection with such Xenia effects upon yield per acre, extensive physiological and chemical studies should be made of the indirect effects of Xenia upon translocation and net photosynthesis. These suggestions arise from the fact that grain and fodder yields of the recessive sugary and waxy endosperm types are found to respond materially to the effects of Xenia. The importance of these ideas as pertaining to various dent hybrids can be determined only by further research."

Dr. E. C. Rossman of Michigan State University emphasizes the value of further studies of prolific hybrids and genetic diversity as quoted from a recent statement.

"Corn breeding in much of the Corn Belt long discriminated against prolific inbreds and hybrids. Favoritism for large single-eared hybrids dates to the days of hand harvest when farmers preferred to pick only one large ear per plant. Interest in prolific hybrids is now increasing with the objectives that they may (1) yield more than single-ear hybrids at low as well as high plant population, and/or (2) be better adapted to adverse conditions of drouth, low soil fertility, etc. with a lower tendency for barren plants.

"Inbreeding and selection since 1953 in populations of Southern prolific inbreds, hybrids, and open pollinated varieties crossed with early maturing Michigan inbreds has led to a group of two-eared and single-eared inbreds with exceptional combining ability, significantly higher than Wf9 and other elite Corn Belt inbreds. Evaluations in double-cross hybrids at four locations and several plant populations in each of two years, 1960 and 1961, in Michigan have shown that the best two-eared hybrids were not significantly higher

yielding than the best single-eared hybrids involving these inbreds. However, these hybrids average 13.5% and 23.4% higher yields than Michigan 430 and Ohio M15 and were only slightly later in maturity. While we were not able to show that the two-eared hybrids would yield more than the best single-eared hybrids, we did find exciting increases in yield for these new hybrids when compared with current recommended hybrids.

"Plant and ear height was higher and eye appeal was, thus, not up to standards required by much of the seed industry. Too frequently a high yielding experimental hybrid has been discarded because it did not have the "good looks" necessary to meet a sales program. Farmers would do well to choose and judge their corn hybrids based on performance rather than looks or eye appeal.

"Genetic diversity among inbred lines has long been recognized as basic for the best yielding corn hybrids. Some of the current cyclic breeding methods eventually lead to closer relationship among the elite inbreds. Use of Southern prolific germ-plasm in Michigan has illustrated the possibilities of further improvement of corn yields through the use of more diverse germ plasm. There is excellent Southern prolific, also non-prolific, germ-plasm that has been well selected for combining ability and other agronomic characteristics that can be readily incorporated with northern germ-plasm. These materials can be utilized more readily than relatively unselected introductions from South America and other areas of the world which may require a longer period of selection and synthesizing of population to become adapted."

Professor G. H. Stringfield, formerly of the U. S. D. A. corn breeding group, who for many years was a leader in Ohio both in basic and applied research also has emphasized the importance of breeding prolific types in the Corn Belt. He has furnished the following statement,

"A wider use of artificial drying of corn on farms and better storage and treatment to eliminate or more completely control the weevil in the South would be of great value."

In conversation with Dr. J. L. Haynes they together concluded that,

"The improvement of cultural methods would reduce seasonal fluctuations in yield in the sub humid easterly states where cold wet soil is often a limiting yield factor. Methods

should be devised to facilitate the establishment of a corn crop in soils and seasons where non friable soil structure would defeat it under present cultural practices. Given these improved cultural practices and germ plasm improvements, a great extension of continuous corn culture will follow."

It should be of great interest to note results from such continuous corn culture with particular reference to the accumulation of soil borne diseases such as the root and stalk rots and to the possible cumulative increase in such pests as the corn root worms.

Dr. J. H. Lonnquist believes it is important to continue the search for better germ plasm as has been pointed out and briefly discussed previously. He is continuing to select by various methodologies such as mass selection, modified ear-to-row methods and recurrent selection for better combinations of genes from outstanding open-pollinated varieties believing that such improved synthetics will play an important part in further breeding programs. He also emphasized the value of genetic diversity of origin and the more complete utilization of exotic germ plasm.

Dr. E. H. Rinke has continued to study the importance of breeding for improved yield components such as length of ear, depth of kernel and prolific types. He states as follows,

"From recent studies of yield components and the more complete utilization of genetic diversity significant progress is being made in producing improved inbreds that in themselves yield much better than the average of inbreds now used in double crosses grown in Minnesota. These improvements in inbreds have led to the development of higher yielding double crosses. Future breeding researches of this nature should lead to marked and continual improvement in double crosses. The eventual wider use of single crosses for the commerical crop seems probable."

Dr. F. A. Loeffel has emphasized the importance to previous and future developments of hybrid corn of the work of a group of cytogeneticists and geneticists. These would include such workers as Emerson, Stadler, Rhoades, Burnham, Brink, Randolph and McClintock. It seems unnecessary here to emphasize individual contributions. Suffice it to say that continued genetical and cytogenetical research will without doubt prove of both basic and applied importance in relation to corn breeding. This would seem a logical continuation of basic studies such as

those carried out earlier by East, Shull, Richey, Jones, Jenkins, Lindstrom and the writer. Dr. H. H. Kramer has suggested also that research work at the experiment stations will revert to the same type of fundamental approach that made hybrid corn possible.

Dr. Fred H. Hull suggested that a better basic understanding of the genetics of heterosis, together with a more efficient breeding plan designed on the basis of that knowledge, would be an important future development.

Glenn Smith suggested the isolation of sweet corn inbreds bearing ears that remain in edible condition over an extended period.

Dr. L. A. Tatum emphasized the importance of a more clear recognition of needs or goals that have not yet occurred to us.

The writer greatly doubts his own ability as a prophet. It does seem evident from this rather brief review of future possibilities in hybrid corn development that great advances will be made in the future. It may be that none will be as spectacular as the development of the hybrid corn concept which has been the basis of this story. However, the value of continued basic and applied research in relation to further hybrid corn development seems very evident. Such research together with close cooperation of research workers with the hybrid seed producer, with the farmer grower and with the needs of the consumer in mind, presents a real challenge to all who have a part in the program of future developments of hybrid corn.

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